CANADIAN JOURNAL OF RESEARCH

VOLUME 28 APRIL, 1950 NUMBER 2

— SECTION D —

ZOOLOGICAL SCIENCES

Contents

Page

Population Cycles and Gene Frequency Fluctuations in Foxes of the Genus *Vulpes*, in Canada—*John B. Calhoun* - - 45

Observations on the Bionomics of Some Northern Mosquito Species (Culicidae: Diptera)—*B. Hocking, W. R. Richards, and C. R. Twinn* - - - - - - - - - - - - - 58

Larvae of Dipterous Parasites of Nymphal and Adult Grasshoppers—*R. W. Smith and Thelma U. Finlayson* - - - 81

NATIONAL RESEARCH COUNCIL
OTTAWA, CANADA

CANADIAN JOURNAL OF RESEARCH

The *Canadian Journal of Research* is issued in six sections, as follows:

A. Physical Sciences	D. Zoological Sciences
B. Chemical Sciences	E. Medical Sciences
C. Botanical Sciences	F. Technology

For the present, Sections A, C, D, and E are to be issued six times annually, and Sections B and F, twelve times annually, each under separate cover, with separate pagination.

The *Canadian Journal of Research* is published by the National Research Council of Canada under authority of the Chairman of the Committee of the Privy Council on Scientific and Industrial Research. The *Canadian Journal of Research* is edited by a joint Editorial Board consisting of members of the National Research Council of Canada, the Royal Society of Canada, and the Chemical Institute of Canada.

Sections B and F of the *Canadian Journal of Research* have been chosen by the Chemical Institute of Canada as its medium of publication for scientific papers.

EDITORIAL BOARD

Representing
NATIONAL RESEARCH COUNCIL

DR. H. P. ARMES (*Chairman*),
Dean of the University,
University of Manitoba,
Winnipeg, Man.

*DR. G. H. HENDERSON,
Professor of Mathematical Physics,
Dalhousie University, Halifax.

DR. ROBERT NEWTON,
President, University of Alberta,
Edmonton, Alta.

DR. C. H. BEST,
The Banting and Best Department of Medical Research,
University of Toronto, Toronto.

Representing
ROYAL SOCIETY OF CANADA

DR. A. NORMAN SHAW,
Chairman, Department of Physics,
McGill University, Montreal.

DR. J. W. T. SPINKS,
Head, Department of Chemistry,
University of Saskatchewan,
Saskatoon.

Section III

DR. H. S. JACKSON,
Head, Department of Botany,
University of Toronto, Toronto.

DR. E. HORNE CRAIGIE,
Department of Zoology,
University of Toronto,
Toronto.

Section V

Ex officio

DR. LÉO MARION, Editor-in-Chief,
Division of Chemistry,
National Research Laboratories,
Ottawa.

DR. H. H. SAUNDERSON,
Director, Division of Information Services,
National Research Council.
Ottawa.

Representing
THE CHEMICAL INSTITUTE OF CANADA

DR. H. G. THODE,
Department of Chemistry,
McMaster University,
Hamilton.

EDITORIAL COMMITTEE

Editor-in-Chief,	DR. LÉO MARION
Editor, Section A,	DR. A. NORMAN SHAW
Editor, Section B,	DR. J. W. T. SPINKS DR. H. G. THODE
Editor, Section C	DR. H. S. JACKSON
Editor, Section D,	DR. E. HORNE CRAIGIE
Editor, Section E,	DR. J. B. COLLIP
Editor, Section F,	DR. J. A. ANDERSON DR. A. NORMAN SHAW DR. H. G. THODE

Manuscripts should be addressed:

Editor-in-Chief,
Canadian Journal of Research,
National Research Council, Ottawa, Canada.

**Deceased.*

Canadian Journal of Research

Issued by THE NATIONAL RESEARCH COUNCIL OF CANADA

VOL. 28, SEC. D. APRIL, 1950 NUMBER 2

POPULATION CYCLES AND GENE FREQUENCY FLUCTUATIONS IN FOXES OF THE GENUS *VULPES*, IN CANADA[1]

BY JOHN B. CALHOUN[2]

Abstract

Population densities of foxes of the genus *Vulpes* over most of Canada have shown a fairly regular 9 to 10 year cycle upon which has been superimposed a trend toward increase in numbers. These changes in density are investigated with reference to changes in frequency of the two genes that determine the presence of black rather than red pigment of the pelage. Of the 14 27-year series of gene frequency data, only two show any apparent correlation with the 9 to 10 year cycle in population density. These two, each with a negative correlation whose probability is less than .001, are for the "Alaskan black" gene in the North West Territories and for the "Canadian black" gene in Quebec. On the basis of these latter data the hypothesis is forwarded that there is some selective factor that may operate against these two "black" genes in an expanding population and may favor their increase in frequency when the population is decreasing in size. It is believed that this hypothesis is sufficient to explain the gradual decrease in gene frequency associated with the gradual increase in the size of the population. This hypothesis is utilized to explain the east–west gradient in gene frequency on the basis of negative selection from presumed eastern and western glacial refugia.

Introduction

Colored foxes occur in three main phenotypes: red, cross, and silver. Each is actually a composite phenotype of two or more genotypes resulting from a two-factor type of inheritance (Warwick and Hanson, 1937 (10)). Among wild populations, analysis of the annual fur accessions of the Hudson's Bay Company has already shown a few of the patterns of occurrence of these three phenotypes.

During the past few decades the percentage of silver foxes in the total catch of colored foxes has been steadily declining (Elton, 1942 (4), Fig. 15; Butler, 1945 (1), Fig. 2). Haldane (1942 (7)) has constructed an hypothesis to account for the decline in the proportion of silver foxes due to selective action of man in shooting proportionately more silver than red foxes. Although there are no quantitative data on selective shooting, Butler presents arguments indicating that selective shooting in recent years is inadequate to explain the continual decline of silver foxes.

Butler (1945 (1)) suggests another reason for the decline in the percentage of silver foxes taken in Canada. In southern Canada and the northern United

[1] *Manuscript received in original form June 2, 1949, and, as revised January 9, 1950.*

Contribution from the Department of Zoology and Entomology, The Ohio State University, and the Rodent Ecology Project of the Department of Parasitology, School of Hygiene and Public Health, The Johns Hopkins University. The work reported in this paper was partially conducted under a grant from the International Health Division of the Rockefeller Foundation.

[2] *Address of the author: Roscoe B. Jackson Memorial Laboratory, Bar Harbor, Maine.*

[The February issue of Section D (Can. J. Research, D, 28 : 1-43. 1950) was issued February 24, 1950.]

Canadian Journal of Research

Issued by THE NATIONAL RESEARCH COUNCIL OF CANADA

VOL. 28, SEC. D. APRIL, 1950 NUMBER 2

POPULATION CYCLES AND GENE FREQUENCY FLUCTUATIONS IN FOXES OF THE GENUS *VULPES*, IN CANADA[1]

BY JOHN B. CALHOUN[2]

Abstract

Population densities of foxes of the genus *Vulpes* over most of Canada have shown a fairly regular 9 to 10 year cycle upon which has been superimposed a trend toward increase in numbers. These changes in density are investigated with reference to changes in frequency of the two genes that determine the presence of black rather than red pigment of the pelage. Of the 14 27-year series of gene frequency data, only two show any apparent correlation with the 9 to 10 year cycle in population density. These two, each with a negative correlation whose probability is less than .001, are for the "Alaskan black" gene in the North West Territories and for the "Canadian black" gene in Quebec. On the basis of these latter data the hypothesis is forwarded that there is some selective factor that may operate against these two "black" genes in an expanding population and may favor their increase in frequency when the population is decreasing in size. It is believed that this hypothesis is sufficient to explain the gradual decrease in gene frequency associated with the gradual increase in the size of the population. This hypothesis is utilized to explain the east–west gradient in gene frequency on the basis of negative selection from presumed eastern and western glacial refugia.

Introduction

Colored foxes occur in three main phenotypes: red, cross, and silver. Each is actually a composite phenotype of two or more genotypes resulting from a two-factor type of inheritance (Warwick and Hanson, 1937 (10)). Among wild populations, analysis of the annual fur accessions of the Hudson's Bay Company has already shown a few of the patterns of occurrence of these three phenotypes.

During the past few decades the percentage of silver foxes in the total catch of colored foxes has been steadily declining (Elton, 1942 (4), Fig. 15; Butler, 1945 (1), Fig. 2). Haldane (1942 (7)) has constructed an hypothesis to account for the decline in the proportion of silver foxes due to selective action of man in shooting proportionately more silver than red foxes. Although there are no quantitative data on selective shooting, Butler presents arguments indicating that selective shooting in recent years is inadequate to explain the continual decline of silver foxes.

Butler (1945 (1)) suggests another reason for the decline in the percentage of silver foxes taken in Canada. In southern Canada and the northern United

[1] *Manuscript received in original form June 2, 1949, and, as revised January 9, 1950.*

Contribution from the Department of Zoology and Entomology, The Ohio State University, and the Rodent Ecology Project of the Department of Parasitology, School of Hygiene and Public Health, The Johns Hopkins University. The work reported in this paper was partially conducted under a grant from the International Health Division of the Rockefeller Foundation.

[2] *Address of the author: Roscoe B. Jackson Memorial Laboratory, Bar Harbor, Maine.*

[The February issue of Section D (Can. J. Research, D, 28 : 1-43. 1950) was issued February 24, 1950.]

States the genes that determine the occurrence of the silver color phases have a lower frequency than to the north. Migration northward of the southern types may have produced the observed decrease in the percentage of silver foxes. The increase in the numbers of foxes concomitant with the increase in acreage of farmland, which provides more habitat for foxes, may have produced the impetus for such a migration. Although there are no data to show that such an extensive northward migration of southern types has occurred, Butler (1947)(2)) shows rather clearly that in the North West Territories both northward and southward movements must occur to explain the rapid and random fluctuations that occur in gene frequencies.

Butler (1945 (1)) has also shown that there are east–west gradients in gene frequency, which extend clear across the continent. This leaves us with four main facts concerning change or condition of the heredity in wild populations of foxes: (1) decrease in percentage of silver foxes; (2) random local changes in gene frequency due to migration of foxes; (3) north–south gene frequency gradients; (4) east–west gene frequency gradients.

The development of these gradients in space and time remain inadequately explained. The study here reported was made in the hope that any changes in gene frequency that might occur during the regular 9 to 10 year population density cycle might aid in the understanding of these gene frequency gradients, which must have been established many hundreds or thousands of years ago. The writer is greatly indebted to the Hudson's Bay Company and Dr. L. Butler for providing the data for analysis. The data provided consisted of tabulations of the numbers of the three main color phases or phenotypes taken each year from seven of the provinces from 1916 to 1943, 1944, and 1945. Over 600,000 specimens were represented in these data.

Inheritance of the Color Phases and Calculation of Gene Frequency

Vulpes occurs in three color phases, red, cross, and silver. Kellogg (1941 (9)) presents data that indicate that the amount of white in the guard hairs is modified by several allelic series of gene modifiers. Here we shall not be interested in such modifying genes or in several other mutant genes isolated in fox breeding farms. Our attention will be focused on the hereditary mechanism responsible for the three principle phenotypes occurring in the wild. In the main, they result from the replacement of red by black pigment and the extent of black pigment in the hairs. Cross (1941 (3)) suggested that a single pair of genes was responsible for the color inheritance, but Butler (1945 (1)) has shown that only in British Columbia will a one factor hypothesis explain the observed ratios. In all the rest of Canada some additional hereditary factors must be involved in modifying the ratios. Butler accepts the alternative hypothesis forwarded by Warwick and Hanson (1937 (10)) of a two factor inheritance where there is no dominance. This inheritance along with Butler's equations for the three composite phenotypes is reproduced below.

Genes:	B and its allele b;*		A and its allele a.†	
Frequency of genes:	p and	q;	m and	n.
Phenotypes and their frequency:		BB	Bb	bb
		p^2	$2pq$	q^2
	AA	$AABB$	$AABb$	$AAbb$
	m^2	Red	Smoky red	Silver
		p^2m^2	$2(pq)m^2$	m^2q^2
	Aa	$AaBB$	$AaBb$	$Aabb$
		Cross	Cross	Silver
	$2mn$	$2(mn)p^2$	$4mnpq$	$2(mn)q^2$
	aa	$aaBB$	$aaBb$	$aabb$
		Silver	Silver	Silver
	n^2	p^2n^2	$2(pq)n^2$	n^2q^2

"This gives: red $p^2m^2 + 2(pq)m^2$
cross $2(mn)p^2 + 4mnpq$
silver $1 -$ (reds + cross)"

Butler says: "Working with various values of "p" and "m" we have found frequencies of A and B which fit all ratios". Although he arrived at close approximations of the gene frequency by the empirical method used by him it is possible to calculate accurately the exact theoretical gene frequencies as follows:‡

Let the frequency of the red color phase $= R$

Let the frequency of the cross color phase $= C$

Then from the upper horizontal line in the above grid it is seen that:

$$m^2 = R + m^2q^2$$

And from the middle horizontal line:

$$2mn = C + 2(mn)q^2$$

Respectively from the above we have:

$$1 - q^2 = R/m^2$$

and

$$1 - q^2 = C/2mn$$

Equate and substitute $1 - n$ for m,

Then

$$n = C/(C + 2R)$$

$m = 1 - n$ (the frequency of gene a)

* *The "Canadian" gene.*

† *The "Alaskan" gene.*

‡ *These calculations were made without taking into consideration the frequency of silver foxes, Dr. C. P. Winsor has checked these calculations using the frequencies of all three genotypes. By this method the same values for m and p result as here given.*

Returning to the first equation listed:

$$m^2 = R + m^2q^2$$

Therefore:

$$q^2 = \frac{m^2 - R}{m^2}$$

$$q = \sqrt{\frac{m^2 - R}{m^2}}$$

$p = 1 - q$ (the frequency of gene *b*)

With these equations the theoretical values of gene frequencies of any one year's yield may be determined. It has been noted that the foxes in British Columbia lack some of the hereditary material possessed by foxes in most of the rest of Canada. The gene lacking is gene *b*. Gene *B* then has a 100% frequency. When *b* is absent it is impossible to solve the equation for *q*. Therefore, whenever *q* fails to solve, *b* is known to be absent and *m* and *n* may be determined by taking the square root of the observed frequencies of red pelts and silver pelts.

Whenever either gene *a* or gene *b* is homozygous black pigmented (silver) foxes occur. Silver foxes with the genotype *aaBB* occur most frequently in Alaska. Gene *a* will be referred to as the Alaskan gene. Silver foxes of the genotype *AAbb* occur most abundantly in eastern Canada. Gene *b* will be referred to as the Canadian gene.

Hypothetical Relationships

Butler (1945 (1)) has shown that one of the genes responsible for black rather than red pigmented hair decreases from the west coast of Canada to the east coast, whereas another gene with a similar effect shows just the opposite trend of change in gene frequency. It was the occurrence of these two opposite transcontinental trends in gene frequency that provided the stimulus for further effort on the part of the present writer to explain their occurrence. These trends suggested that after the last glacial period foxes spread across Canada from refugia on either the west or the east side of the continent or both. If the recolonization of the previously ice-covered terrain occurred from both an easterly as well as a westerly direction it would seem that some factor associated with the gradually expanding population was deleterious to the survival of foxes possessing these "black-fur" genes. Had the recolonization occurred from only one side of the continent it would be necessary to postulate that one gene was favored and the other was removed as the foxes recolonized the glaciated portion of North America. Both of these hypotheses require the assumption that the east–west gradient in gene frequency established shortly after the last glacial period has been maintained essentially unaltered to the present time. Colored foxes in Canada undergo periodic fluctuations in population. Assuming that the conditions that permit an expanding population, whether it be the postglacial reinvasion or the regular

increase following a depressed phase of the 9 to 10 year population cycle, similarly affect changes in gene frequency, it should be possible to determine the relation between trends in size of the population and accompanying changes that occur in gene frequency.

Analysis of Data

Using the equations previously given, the gene frequencies for the samples from each province were calculated. These are plotted along with the log of the population in Figs. 1–7. It will be seen that the fluctuation of the size of the sample population for each province goes through regular alterations. Years of maximum and minimum numbers practically coincide for all provinces.

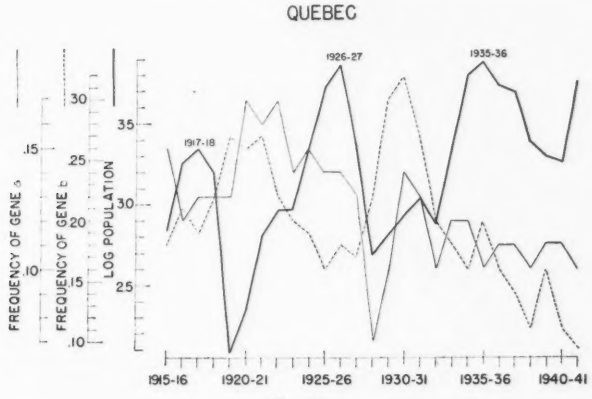


FIG. 1.

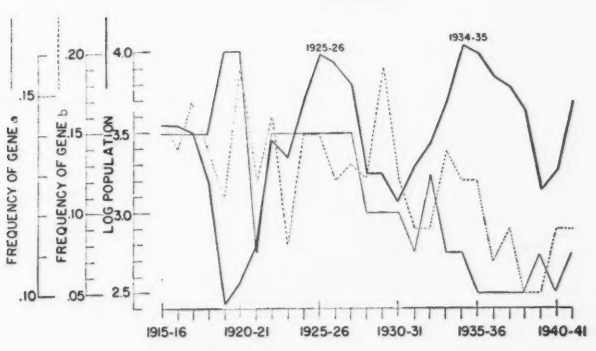


FIG. 2.

The gene frequencies for the North West Territories evince the most regular fluctuations of all the samples studied. The Alaskan gene fluctuates inversely with the population. Although the Canadian gene is not present during all

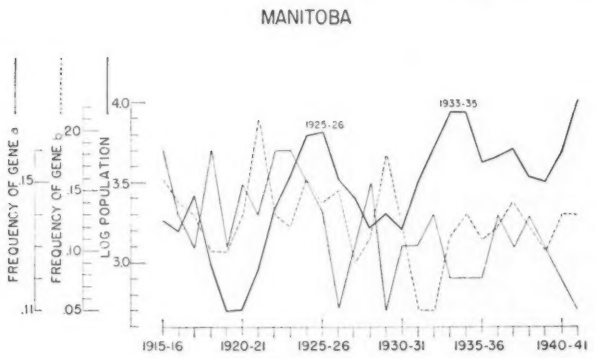


FIG. 3.

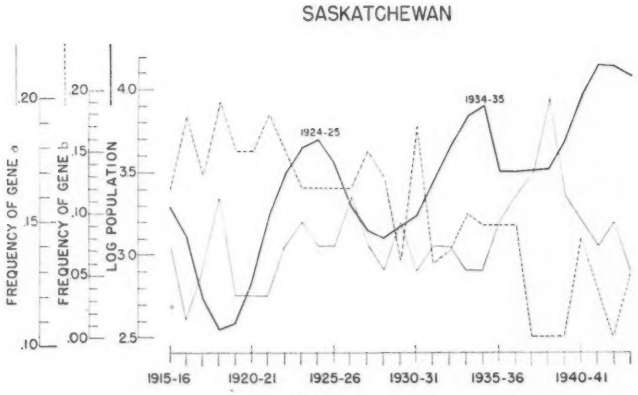


FIG. 4.

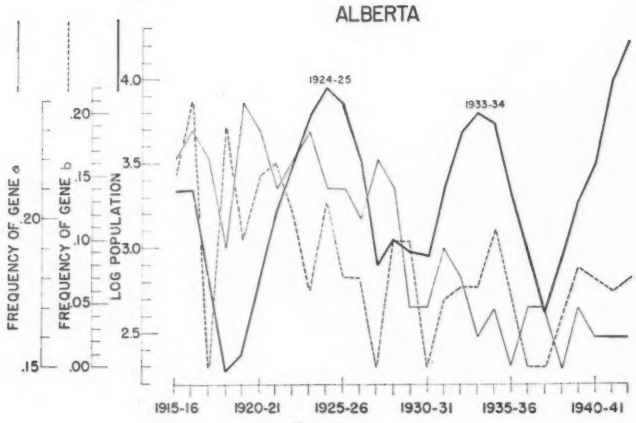


FIG. 5.

the latter years analyzed, those changes in frequency that occur seem to be in the same direction as the changes in the size of the population during similar periods of the cycle.

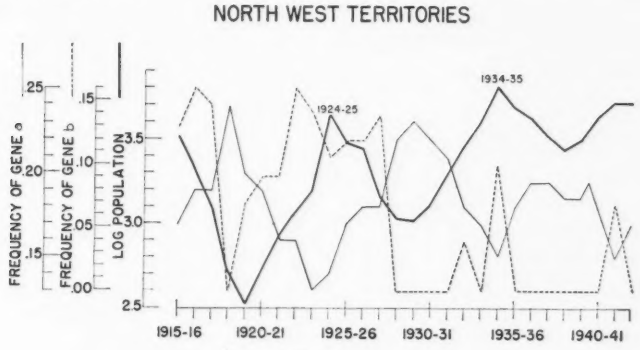


FIG. 6.

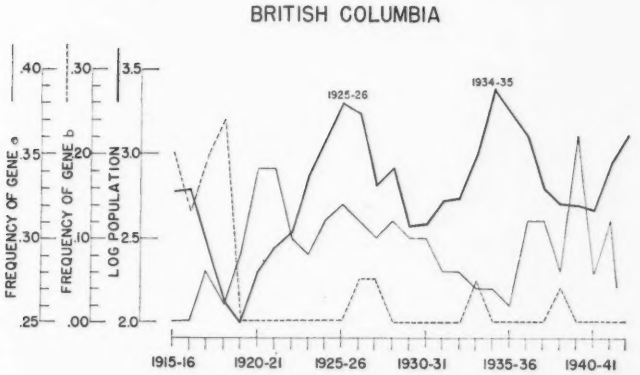


FIG. 7.

There is only one clear-cut visible relationship among the data for the six other areas. This is in Quebec where the frequency of the Canadian gene fluctuates inversely with the fluctuations in size of the population. For most of the seven samples there appears to be a trend of increase in the size of the samples taken, which presumably reflects a gradual increase in the size of the actual population. Gene frequencies gradually decline, despite intermittent periods of increase. Several methods were utilized in searching for possible association of changes in gene frequency with changes in size of the population. Most of these are no more than suggestive of possible correlations. Any really clear-cut and consistent correlation between changes in gene frequency and changes in the size of the population will be revealed in 2×2 tables involving decrease or increase trends of both factors providing there are no irregular

lags in the associations. The χ^2 values for such tables for the population and the Alaskan gene for the same and for the following year, and for the population and for the Canadian gene for the same and for the following year are respectively: 2.76, 1.64, 1.96, and 0.0. No significance of relationship is indicated by these χ^2 values.

There may be trends in the fluctuation of gene frequency associated with fluctuations in the size of the population not revealed in the above analysis. If so, such associations should be most obvious if changes in gene frequency between years of maximum and minimum size of the population are compared. An inspection of the figures (omitting the data for the North West Territories) shows that there is nearly equal likelihood for the frequencies of the Alaskan gene or the Canadian gene to show an over-all increase or decrease between depressions and peaks or between peaks and depressions.

Even if there is no relationship between gene frequency and population size, there may be a relationship between the direction of change of the frequencies of the two genes. The trends in increase or decrease in frequency for the Alaskan and Canadian genes for each year for each province were tabulated. Omitting the data for British Columbia and the North West Territories it was found that during 34 years the gene frequencies fluctuated in the same direction while during 51 years they fluctuated in opposite directions. The probability of this difference occurring by chance was about 0.06. Including the data on the other two provinces the figures become respectively 39 and 66, with the probability of their occurring by random sampling being less than 0.01. This seems to indicate that, irrespective of changes in population size, conditions that favor the increase of one of these genes cause a decrease in the other.

It has been noted above that for the North West Territories there is an apparent regular correlation between change in gene frequency and change in population size. For this reason, further analysis was made of these data. The data for Quebec were used as a contrast since they contained one apparent correlation. Approximate long-time trends were determined by the use of trinomial orthogonals (Fisher and Yates, 1938 (6)). These trends and the deviations of the observed data from these trends are shown in Figs. 8–11. Gene frequencies used in these calculations were carried to the third decimal place.

Using the deviations of the observed data from the theoretical long-time-trend several correlation coefficients were determined. These are given in Table I. The data are clear-cut for the North West Territories. When the population and gene frequency changes are taken the same year the correlations seem to be quite significant. The fluctuation in frequency of the Alaskan gene has a negative correlation with fluctuations in size of the population, whereas the Canadian gene shows a positive similar correlation. Likewise, the negative correlation of the changes in frequency between the two genes is significant. The data for Quebec show fewer significant correlations. There are no significant correlations involving the Alaskan gene. There is a significant negative correlation between fluctuations of the population and the

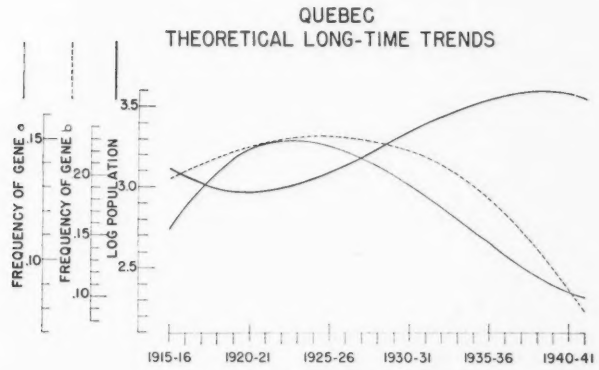


FIG. 8.

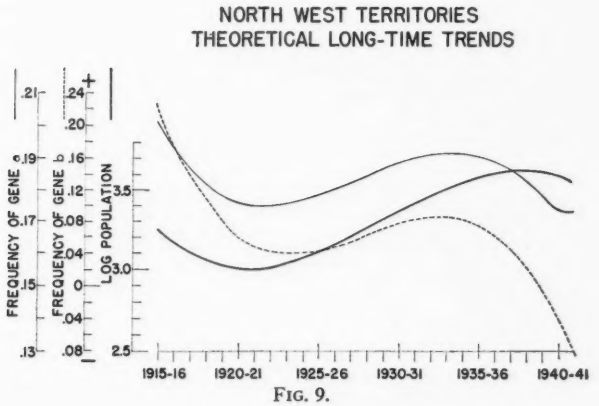


FIG. 9.

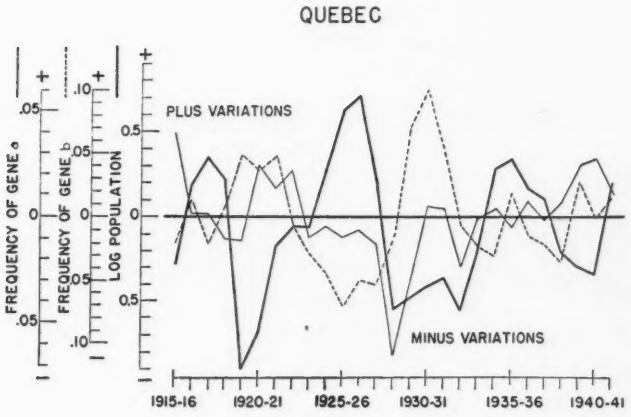


FIG. 10.

Canadian gene in Quebec in contrast to the positive correlation for the North West Territories. It will be noted that although neither correlation determined for the Alaskan gene in Quebec may be considered as being significant, the probability of the significance of r is four times as great when a lag of one year is allowed for the change in gene frequency.

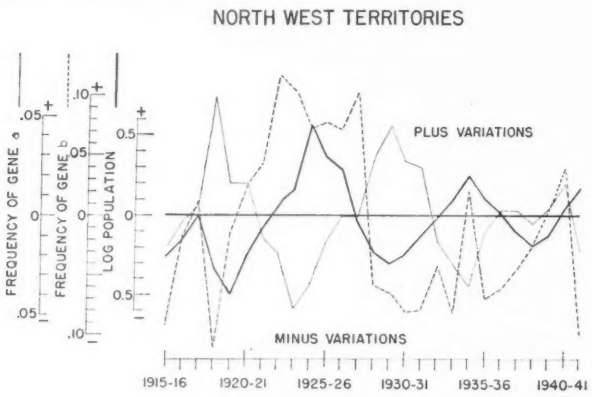


FIG. 11.

TABLE I

CORRELATION ANALYSIS OF GENE FREQUENCY FLUCTUATIONS AND POPULATION FLUCTUATIONS AFTER REMOVAL OF LONG-TIME TRENDS

Factors correlated	North West Territories		Quebec	
	Coefficient of correlation (r)	Probability of t test of r	Coefficient of correlation (r)	Probability of t test of r
1. Population with the Alaskan gene for the same year	−0.645	.001	+0.050	.8
2. Population with the Alaskan gene for following year*	−0.364	.1	−0.306	.2
3. Population with the Canadian gene for same year	+0.584	.01	−0.594	.001
4. Population with the Canadian gene for the following year*	+0.339	.1	−0.582	.01
5. The Alaskan gene with the Canadian gene	−0.480	.01	+0.232	.3

** Population fluctuations are correlated with gene frequency fluctuations of the following year, since such a lag in gene frequency change might be expected if the conditions that cause the change in the size of the population of one year induce a differential survival of progeny of differing genotypes during the following breeding period.*

Discussion

The data as a whole show no consistent regularity of association of gene frequency change with population fluctuation. However, it is important to note the conditions under which very significant correlations occur between

trends of change in gene frequency and population size. In Quebec gene *b* reaches its highest frequency, whereas gene *a* reaches its lowest frequency. Here the Canadian gene *b* shows a marked tendency to fluctuate inversely in frequency with the population size. Likewise, in the North West Territories where the gene *a* has a high frequency and gene *b* a low frequency, this Alaskan gene *a* also shows a marked tendency to fluctuate in frequency inversely with the population.

The third fairly regular association of change refers to the tendency of the frequency of the two genes to fluctuate in opposite directions from one year to the next. It may well be that this mutual antagonism between these two genes, if it may be so designated, masks the tendency for their frequency to be negatively correlated with changes in population size in the more centrally located provinces where their frequencies are more nearly equal. This antagonism may account for the fact that gene *b* seems to show a positive rather than a negative correlation with the population change in the North West Territories (see Table I).

Why the frequency of the Alaskan gene *a* fails to show any regular fluctuation in British Columbia in association with the population cycle is unknown. Here one would expect the most marked correlation since the frequency of gene *a* is higher than anywhere else in Canada and gene *b* is practically absent. It may be pointed out that the samples from British Columbia are relatively small and thus are more subject to random errors in sampling. If the population is really more sparse there is also greater chance for irregular shifts to occur from gene drift (Wright, 1940 (11, pp. 161–183)).

The Hudson's Bay data give no evidence of the manner in which this selection, which produces the alterations in gene frequency, occurs among foxes. Hanson's original data upon which the two factor hypothesis was proposed have been lent to me for examination by the U.S. Department of Agriculture through the courtesy of Mr. Charles Kellogg. With two exceptions these extensive data on results of crosses on fox farms confirm the two factor hypothesis. The two exceptions also lend light on the possible time of occurrence of selection among the genes involved.

They are: 1. $AAbb \times AaBb$ with a total of 216 progeny, which should give an expected ratio of 54 smoky reds, 54 cross, and 108 silver, whereas the observed distribution was respectively 45 : 71 : 100. The great reduction was in smoky reds. In this cross, gene *a* showed an increase in frequency of .033 from the expected, whereas gene *b* showed a decrease in frequency of .021.

2. $AABb \times AAbb$ with a total of 224 progeny, which should give an expected ratio of 112 smoky reds and 112 silver, whereas the observed distribution was respectively 99 : 125. Here again there were fewer smoky reds than expected. Gene *A* being homozygous could show no change in frequency, but gene *b* showed an increase in frequency of .05 from the expected.

These fox-farm breeding data indicate that there may be an *in utero* selection (competition) between different genotypes. It also supports the conclusion

that there is some mutual antagonism between genes *a* and *b*. No significant difference was found in the mean size of litters produced by any maternal genotypes in the total of over 700 litters included in the Hanson data.

Assuming that the conclusion, derived from the recent data, that both the Alaskan gene *a* and the Canadian gene *b* tend to increase in frequency under conditions that reduce the size of the population, and to decrease in frequency when the population expands, is correct, let us see how it may assist in interpreting the current distribution of these genes. It is logical to assume that, during the last interglacial period, colored foxes of the genus *Vulpes* were distributed roughly as they are today. This means that they ranged over most of North America. With the coming of the Wisconsin glaciation the largest surviving population should have occurred in what is now central and southern United States. As is now the case over this area, there were probably very few silver and cross foxes, thus a low frequency of genes *a* and *b*.

Within or north of the glaciated region there were few and limited areas where foxes might have survived. Extensive studies have been made of the flora of these unglaciated regions by Fernald (1925 (5)) and Hulten (1937 (8)). Their studies indicate that the flora was rather diversified containing many grasses, herbaceous plants, and a few trees. It seems to have been sufficient to assume that it may have supported an adequate fauna from which foxes could have survived. The main refugia during glacial times in the northeast center about the Gaspé peninsula and in the northwest in Alaska, Queen Charlotte Islands, and scattered localities in the mountains of British Columbia. If our hypothesis is correct, the genes *a* and *b*, which produce the black pigment, would have become greatly increased in frequency during glacial times when relatively small populations occurred in the refugia. With the retreat of the glaciers both the eastern and western populations expanded into the central mass of the continent producing the present east–west gradients as a result of selection in an expanding population favoring the red genes *A* and *B*. At the same time foxes from the large southern population, which contained few of the black genes *a* and *b*, spread northward producing the observed north–south gene gradient.

With the exception of the data from Quebec and the North West Territories changes in gene frequency in the other provinces appear to be random with little relationship to the population changes occurring on a regular 9 to 10 year basis. Since these provincial samples no doubt constitute an aggregation of isolated or semi-isolated populations between which migration may upset any regular trend of gene frequency change as Butler has shown, one is hardly surprised to find them failing to show any regular pattern of gene frequency when lumped together. Nevertheless, in each of the samples both the Canadian gene *b* and the Alaskan gene *a* gradually declines in frequency accompanying the gradual increase in the size of the population.

It is the opinion of the writer that it is more logical to assume that the reduction in frequency of the black genes in recent years results from the

conditions that favor population increase than to speculation on the effectiveness of selective shooting. Of course, the hypothesis of the effect of recolonization following glaciation on gene frequency can never be truly affirmed, but it is well to keep this proposal in mind when analyzing gene frequencies among foxes. The question of relationship between the 9 to 10 year population cycle is quite another matter. Further detailed analyses of local posts as Butler (1947 (2)) has done may reveal additional confirmation of this hypothesis. However, the greatest contribution to this problem may be made by an investigator who is in a position to study the ecology and genetic changes of a local population through the course of one of its regular fluctuations in population density.

References

1. BUTLER, L. Distribution and genetics of the color phases of the red fox in Canada. Genetics, 30 : 39-50. 1945.
2. BUTLER, L. The genetics of the colour phases of the red fox in the Mackenzie River locality. Can. J. Research, D, 25 : 190-215. 1947.
3. CROSS, E. C. Colour phases of the red fox (*Vulpes fulva*) in Ontario. J. Mammal. 22 : 25-39. 1941.
4. ELTON, E. S. Voles, mice and lemmings. Oxford: Clarendon Press. 1942.
5. FERNALD, M. L. Persistence of plants in unglaciated areas of boreal America. Mem. Am. Acad. Arts Sci. 15(3) : 239-342. 1925.
6. FISHER, R. A. and YATES, F. Statistical tables. Oliver and Boyd Ltd., London. 1938.
7. HALDANE, J. B. S. The selective elimination of silver foxes in eastern Canada. J. Genetics, 44 : 296-304. 1942.
8. HULTEN, ERIC. Outline of the history of arctic and boreal biota during the Quaternary period. Bokforlags Aktiebolaget Thule, Stockholm. 1937.
9. KELLOGG, CHAS. E. Inheritance of degree of silvering in foxes. U.S. Fish Wildlife Service, Wildlife leaflet 178. 1941.
10. WARWICK, B. L. and HANSON, K. B. Yearbook of agriculture, U.S. Dept. Agr. 1937 : 1388-1394. 1937.
11. WRIGHT, S. The statistical consequences of Mendelian heredity in relation to speciation. *In* The new systematics *by* J. Huxley. Oxford: Clarendon Press. 1940.

OBSERVATIONS ON THE BIONOMICS OF SOME NORTHERN MOSQUITO SPECIES (CULICIDAE: DIPTERA)[1]

By B. Hocking,[2] W. R. Richards,[3] and C. R. Twinn[3]

Abstract

The species of mosquitoes now known to occur at Churchill, Man., are listed and include 12 species of Culicinae and four of Chaoborinae. Evidence is advanced that one of these, *Aedes communis* DeG., may really be two species; and a method is suggested of separating some of the black-legged species of *Aedes* without using larval characters or scaling. Some observations on larval habits and habitats, seasonal development, species associations, temperature relationships, and natural enemies are given. Rearing methods used in the field and in the insectary are described. Seasonal changes in numbers, species composition, and activity of the adult population are studied, and quantitative estimates of the influence of meteorological factors on activity are made. Mating habits are described, and adult feeding habits, both on nectar and on blood, are discussed and illustrated. Observations on the development and number of eggs of some species are recorded.

Introduction

During 1947 and 1948, studies of biting flies and their control were carried out at Churchill, Man., as a joint project of the Division of Entomology, on behalf of the Canadian Defence Research Board, and the U.S. Bureau of Entomology and Plant Quarantine, on behalf of the U.S. Army Committee on Insect and Rodent Control. A preliminary account of the mosquitoes of the region based on observations in 1947 has already been published (17). This paper gives further information on the bionomics of the species concerned, derived mainly from the studies in 1948. Other publications arising from the joint investigations are included in the list of references (4, 5, 9, 10, 16).

The Weather

In general, the spring season at Churchill started much earlier in 1948 than in 1947 (17), but cold weather early in June retarded development so that by early July conditions were comparable with those obtaining at the same time in 1947, although much drier. This dryness may have accounted for the rather smaller populations of mosquitoes in 1948 than in 1947.

The ice went out of the Churchill River on June 14, as compared with June 20 in 1947 and June 15 as the mean date for this occurrence.

An analysis of the daily weather summaries obtained from the Dominion Department of Transport meteorological office at Churchill for the period from May 1 to Aug. 15 gives the following figures:

Average temperature for the whole period was 45° F.; for May, 29° F.; for June, 43° F.; for July, 56° F.; and for the first half of August, 61° F. The

[1] *Manuscript received January 4, 1950.*

[2] *Assistant Professor of Entomology, University of Alberta, Edmonton, Alta.*

[3] *Division of Entomology, Science Service, Department of Agriculture, Ottawa; Canada.*

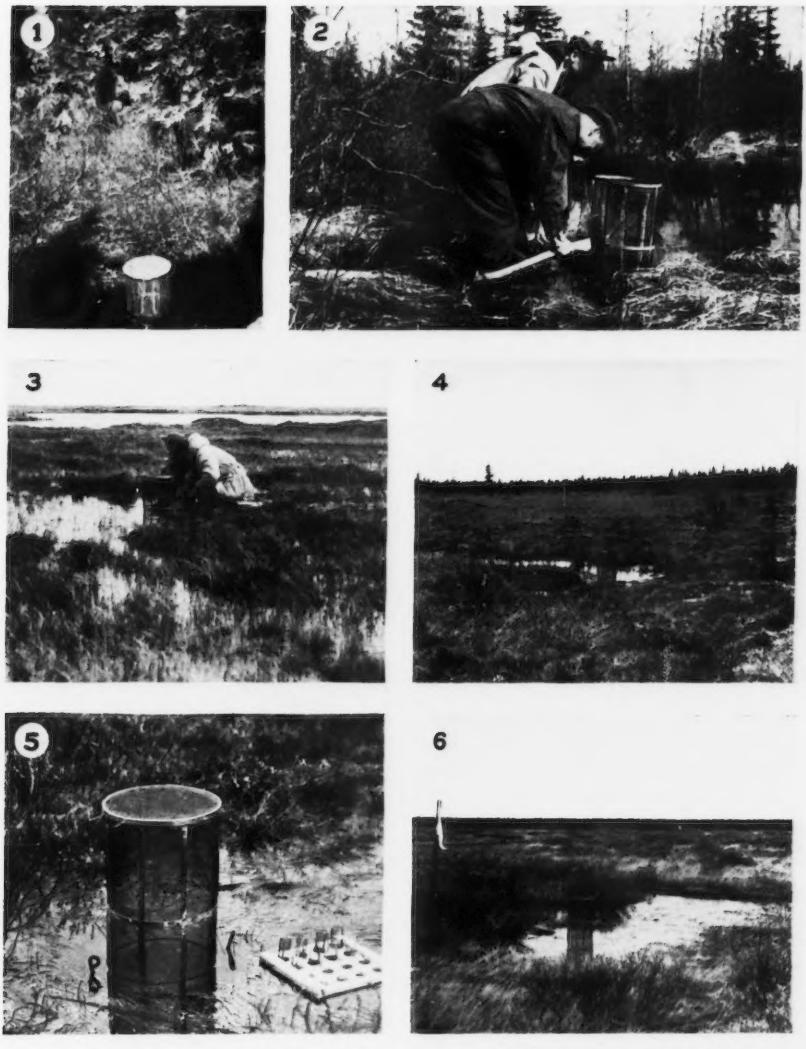


FIG. 1. *Forest Station O.* FIG. 2. *Forest Station A.* FIG. 3. *Tundra Station F.* FIG. 4. *Tundra Station H.* FIG. 5. *Birch–willow Station K.* FIG. 6. *Birch–willow Station M.*

FIG. 7. *Aedes nearcticus feeding on man, stage one, 1½ min.* FIG. 8. *A. nearcticus feeding on man, stage two, 2½ min.* FIG. 9. *A. punctor preparing to feed on flowers of Habenaria hyperborea.* FIG. 10. *Insectary at Churchill, and penguin used for transport in swampy terrain.*

highest temperature recorded was 83° F., on Aug. 12, and the lowest 15° F., on May 6 and again on May 8. The total range of temperature was therefore 68 Fahrenheit degrees.

The average figure for relative humidity for the whole period was 82%; for May 87%; for June, 83%; for July, 81%; and for August, 75%. There was a range of 64%, from 36% on Aug. 3 to 100% on several days. Daily averages ranged from 59% on June 17 to 100% on June 3.

The wind speed ranged from calm on May 31, June 17, July 16 and 17, and Aug. 3 and 10 to 38 miles per hour from the northwest on May 25, and 36 m.p.h. from the north on July 19. The average for May was 13 m.p.h., for June and July each 14 m.p.h., and for August 10 m.p.h., giving an average for the whole period of 12 m.p.h.

The total precipitation during the three and one-half months was 6.75 in., of which 0.45 in. was in the form of snow. Rainfall was as follows: 0.37 in. on five days in May; 1.58 in. on seven days in June; 4.61 in. on 11 days in July, and 0.1 in. on one day in the first half of August. The greatest rainfall on any one day was 2.84 in., on July 30.

The Mosquito Species at Churchill

The following species of mosquitoes have now been recorded as occurring in the vicinity of Churchill, Man.:

Culicinae:

Aedes nearcticus Dyar
nigripes Zett.
punctor Kby.
communis DeG.
excrucians Wlk.
campestris D. & K.
flavescens Müller

Chaoborinae:

Chaoborus nyblaei Zett.
**crystallinus* DeG.
Aedes cinereus Meig.
**spencerii* Theo.
**riparius* D. & K.
Culiseta alaskaensis Ludl.
impatiens Wlk.
**Eucorethra underwoodi* Und.
**Mochlonyx culiciformis* DeG.

The species marked with an asterisk were recorded at Churchill for the first time in 1948; the remaining species were recorded in 1947, and adequate introductory information on them has already been given (17). The immature stages of *A. flavescens*, *A. cinereus*, and *Culiseta* spp. were not taken in 1947; this deficiency was filled in 1948 except for *C. impatiens*. The immature stages of the newly recorded species, except for those of *A. spencerii*, were also found.

The larvae of *A. flavescens* were taken at Stations M and P, details of which are given in the section on field rearing. They were also taken on July 8 from a muck-bottomed pool with mossy margins, in the Warkworth Creek area, and on June 14 from another station in the Beech Bay area (Fig. 11). These pupated on July 17 and 25 respectively, and emerged on July 23 and July 30.

The larvae of *A. cinereus* were first taken from a pool in the Warkworth Creek area, full of debris, dead grasses, and muck, and with a rank growth of grasses and sedges. These were in the fourth instar when taken on July 8, they pupated on July 9, and adults emerged on July 14. Further pupae were

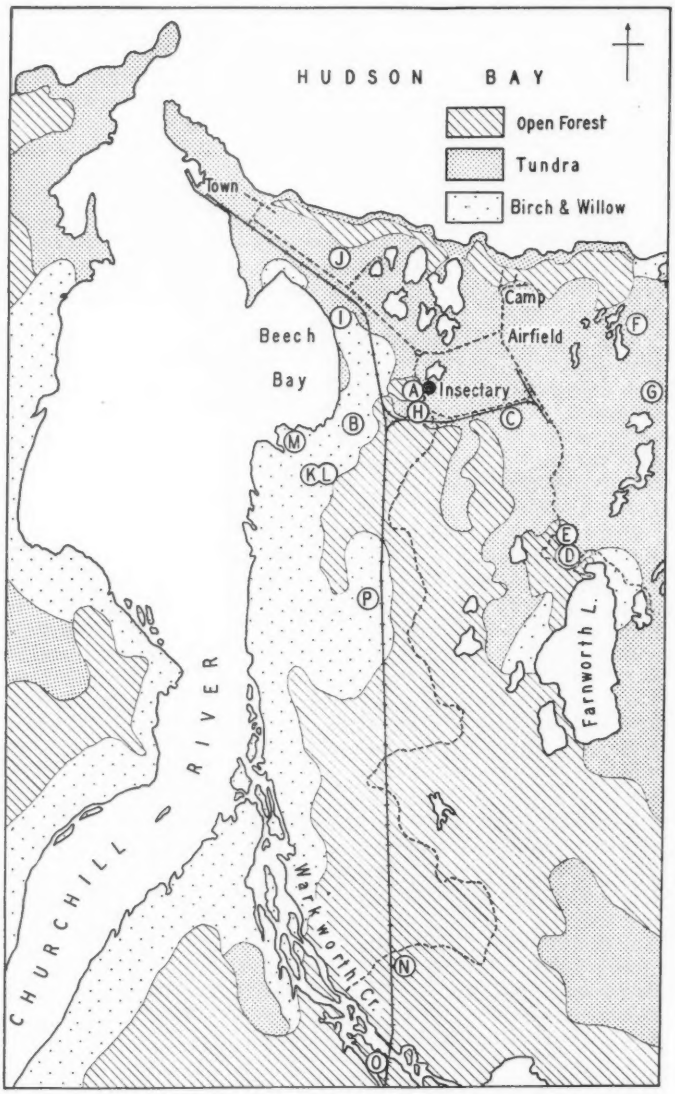


FIG. 11. *Map showing the location of mosquito study stations at Churchill, Man. in relation to vegetation. Scale, 1 in. = approx. 2 miles.*

collected from similar pools in the same locality on July 21, adults emerging on July 22.

The larvae of *Culiseta alaskaensis* were also first taken in the Warkworth Creek area, from a rather small pool overhung with willow and spruce on one side, densely grown up with sedges on the other, and with a dark-brown muck bottom over rock. These were taken as fourth-instar larvae and pupated on the same day, July 21, adults emerging on July 27. Other pupae were collected from similar but larger pools in the same locality up to July 23, pupation occurring as late as Aug. 5 and adults emerging on Aug. 9.

A. spencerii was taken only in the adult stage. Three specimens were taken between May 29 and June 3, considerably earlier than any other species of *Aedes* reached even the pupal stage either in 1947 or in 1948. All three specimens were taken inside army vehicles (Fig. 10). The weather at this time was unusually warm, and winds at speeds up to 22 m.p.h. had been blowing continuously from the south-southeast. It is possible that these specimens came in from farther south, either windborne or on aircraft or trains. The fact that they were taken in vehicles, and that these vehicles were all within easy distance of both the airport and the railway station, suggests the latter explanation. *A. spencerii* is known to be a migratory species, however, and data on the northern limits of its breeding would be very interesting.

Matheson identified *A. nigromaculis* Ludl. among the mosquitoes collected at Churchill by McClure (8) in 1936–7, but this species was not represented in any stage among the material collected either in 1947 or in 1948. A single male specimen of *A. riparius* was reared from a pupa collected on June 27 at Station D. Dr. Alan Stone* identified it from a slide of the genitalia.

Positive identification of the females of the common northern species of *Aedes* with black legs, namely, *nearcticus*, *nigripes*, *punctor*, and *communis*, is not normally possible without the last larval skin and the associated adult with its full complement of hairs and scales. This means that as soon as a mosquito of this group has seen a bit of life, and hence become biologically interesting, it can no longer be specifically identified. In an attempt to eliminate this difficulty, the proboscis length and the wing length of all specimens of this group positively identified by association with the last larval skin were measured. The ratio of proboscis length to wing length for each specimen was calculated, and the frequency distribution of the values of this ratio was plotted for each species (Fig. 12). These curves show that the value of this ratio may be used to separate the majority of specimens of *A. nearcticus* from *A. nigripes*, and with less certainty from *A. punctor*. Separation of *A. nearcticus* from *A. communis* on this basis would seldom be reliable.

The most interesting point that arises from these curves, however, is the appearance of similarly spaced double peaks in the curves for both males and females of *A. communis*, indicating, as has already been suspected, that this may really be two species. On reviewing the original measurements, it was

* *Division of Insect Identification, Bureau of Entomology and Plant Quarantine, Washington, D.C.*

found that the group with the smaller proboscis length/wing length ratio also had the smaller actual measurements. Probably this small form with its habit of developing in enormous numbers in rather special woodland pools

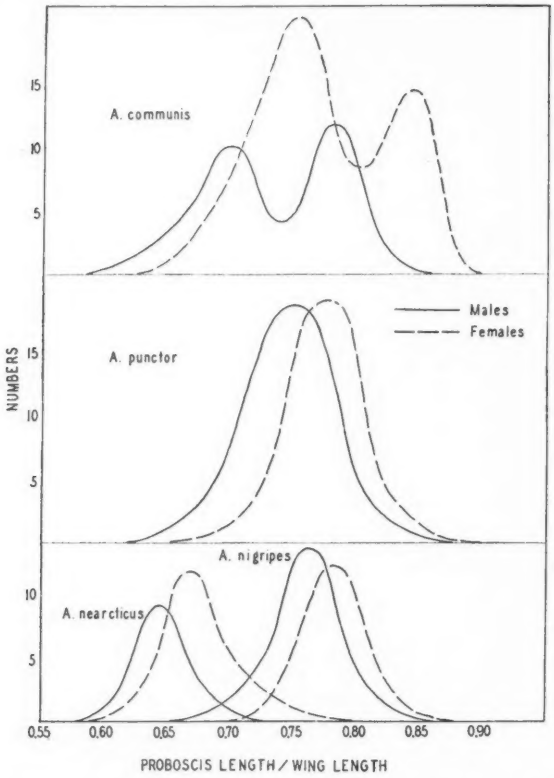


FIG. 12. *Frequency distribution of values for the ratio of proboscis length to wing length of black-legged species of Aedes.*

should be regarded as the true *A. communis* of De Geer, and the larger form as a new species, rather closer in its habits to *A. punctor*. More evidence is required before this can be definitely established.

Of the chaoborine species, single specimens only of *Eucorethra underwoodi* and of *Chaoborus crystallinus* were reared. The former emerged on July 24 from a pupa taken from a small clear pool in deep forest in the vicinity of the insectary on July 21. The latter was collected in the larval stage from a pool in open woodland on June 4; pupation occurred on June 15, and an adult male emerged on June 23. *Mochlonyx culiciformis* was by far the most abundant chaoborine species. Specimens were obtained from Stations C and E, and from a variety of locations in the Warkworth Creek area.

The Immature Stages

General Observations

On account of the difficulties encountered in identifying material collected in 1947 without adequate series of associated males, females, and fourth-instar exuviae, a large amount of rearing was undertaken in 1948, both in the field and in the insectary (Fig. 10) erected about two miles southwest of Churchill military camp. In addition, observations on physical conditions in the pools and on larval activities were made as opportunity offered.

Numerous samples of water, both from pools in which rearing cages were placed and from other characteristic pools, were collected for measurements of pH and salinity. The pH of 52 pools examined ranged from 6.5 to 8.3, the average value being 7.7. The average salinity was approximately 100 p.p.m., expressed as sodium chloride, with a range from 50 to 1200 p.p.m. Determinations of titratable alkalinity agreed well with the pH and salinity combined. The actual data for observation stations are given in Tables I, II, and III.

TABLE I

DATA ON STATIONS IN OPEN SPRUCE–LARCH FOREST

Stn.	Salinity, p.p.m.	pH	Color	Water temp. conditions	Mosquito species	Insectary emergence dates	Duration of pupal period in days:		No. specimens reared from:	
							Range	Mean	Larvae	Pupae
A	1282	7.3	10	Normal	*A. communis*	June 23–30	4–8	4.9	8	—
					A. punctor	June 24	6	—	1	—
E	50	7.3	3	Normal	*A. nearcticus*	June 15–18	10*	10	23	—
					A. punctor	June 25	9	—	1	—
					A. communis	June 30	—	—	0	1
					A. excrucians	July 4–16	3–5	4.7	10	13
					M. culiciformis	July 1–4	—	—	0	7
N	85	7.0	—	Normal	*A. communis*	—	—	—	—	—
O	—	—	—	Back-ward	*A. communis*	—	—	—	—	—
P*	—	—	—	—	*A. punctor*	June 23–27	3	—	1	1
					A. communis	June 26	—	—	—	2
					A. excrucians	June 30	4	—	1	—
					A. campestris	June 30–July 23	2–7	4.7	28	0

* *Not a typical forest station; see description.*

The eggs of many species of *Aedes* withstand desiccation and extreme cold, and as a general rule do not hatch until they are flooded with water after having been subjected to these conditions. Recently Abdel-Malek (1) has shown that the eggs of *A. trivittatus* require the presence of certain plant hormones in critical concentration for optimum percentage hatch. Eggs

TABLE II

DATA ON STATIONS ON TUNDRA

Stn.	Salinity, p.p.m.	pH	Color	Water temp. conditions	Mosquito species	Insectary emergence dates	Duration of pupal period in days:		No. specimens reared from:	
							Range	Mean	Larvae	Pupae
C	205	7.8	3	Back-ward	*A. nigripes*	June 18–27	3–12	5.9	18	—
					A. nearcticus	June 18–23	5–10	6.7	3	—
					A. communis	June 21–27	3–8	7.4	9	—
					A. punctor	June 23–July 8	2–12	6.4	9	—
					A. excrucians	July 4–19	4–10	5.4	13	—
					M. culiciformis	June 30–July 13	4–6	4.9	17	—
D	67	7.5	5	Normal	*A. nigripes*	June 24	7	7	2	—
					A. punctor	June 23–26	4–7	6.6	7	—
					A. excrucians	June 30–July 7	3–6	5.3	6	6
					A. riparius	June 30	3	—	0	1
F	198	8.5	2	Normal	*A. nigripes*	June 23–25	7–12	8.7	3	0
					A. communis	June 26	5	5	2	0
G	171	8.1	1	Slightly back-ward	*A. nigripes*	June 19–23	3–11	9.3	8	0
					A. nearcticus	June 21	12	—	1	0
					A. punctor	June 23–27	6	6	1	1
H	308	8.1	3	Normal	*A. nearcticus*	June 17	—	—	0	2
					A. punctor	June 17–25	7–16	11.9	10	11
J	342	8.3	2	Advan-ced	*A. nigripes?*	June 23	11	—	1	0

of Churchill species of *Aedes* have been observed to hatch in the laboratory when flooded with water from tundra pools, but no observations with specific plant hormones have yet been made on these species.

In muskeg areas, where ground movements may spread out many yards from every step taken, it was found impossible to approach pools without sending all larvae to the bottom, and the least movement of an observer at the margin of a pool would interrupt their activities. A conspicuous habit of the larvae, especially the tundra species, consists of feeding along the edges of submerged and decaying grasses and sedges in the pools. The sessile microflora and microfauna on this vegetation are being studied. The contents of the alimentary canals of *A. communis* larvae from the Warkworth Creek area consisted of about 50% diatoms, 20% filamentous algae, and 30% mixed debris, including fragments of moss and possibly rotifers and pollen grains.

The larvae of the chaoborine species appear to be important predators of *Aedes* larvae, consuming large numbers of these in the insectary. These predators also feed on fairy shrimps, and are in turn fed upon by the larvae of dytiscid beetles. A fairy shrimp has been taken from the prehensile

TABLE III

DATA ON STATIONS IN BIRCH AND WILLOW SCRUB

Stn.	Salinity, p.p.m.	pH	Color	Water temp. conditions	Mosquito species	Insectary emergence dates	Duration of pupal period in days:		No. specimens reared from:	
							Range	Mean	Larvae	Pupae
B	126	8.1	2	Very advanced	*A. nearcticus*	June 21–23	5–10	6.8	13	—
I	376	7.8	3	Advanced	*A. punctor*	June 29	5	—	1	0
K	280	7.8	5	Normal	*A. nigripes*	June 23	8	—	1	—
					A. nearcticus	June 23	8	8	3	—
L	137	8.1	3	Slightly advanced	*A. punctor*	June 25–26	3–4	3.7	3	—
M	368	8.3	5	Advanced	*A. nearcticus*	June 20–26	5–7	5.5	13	1
					A. nigripes	June 23–29	3–5	3.2	9	10
					A. excrucians	July 1–8	4–6	4.9	18	0
					A. flavescens	July 5–9	5–7	6.1	8	—
					A. campestris	July 21	7	—	1	—

antennae of a *Chaoborus* larva, which was itself held in the mandibles of a larval dytiscid. The larvae of *Eucorethra underwoodi* were also observed to feed on adult black flies that got into difficulties on the surface of pools.

Field Rearing

Large cylindrical cages of copper screen, with open bottoms and detachable screen covers, were fastened in the pools, each with two iron pins (Figs. 1 to 6). These were stocked with larvae by dipping from the rest of the pool to secure a large number of adult mosquitoes and show the succession of species and differences in emergence times of males and females.

Also, wooden floats, each fitted with 16 cylindrical cages, 6 in. long by $1\frac{1}{4}$ in. in diameter, were placed in the pools (Fig. 5), and the cages each stocked with a single larva. The 16-mesh screening of which these were made proved rather open; first- and second-instar larvae could escape, and dytiscid larvae were found to be capable of capturing the larvae through the screening. To prevent this, the cages were covered with cheesecloth, but mortality was so high that these small cages proved of little value. Much of the mortality may have been due to the formation of toxic compounds by electrochemical action between the copper and the solder used to join it. Residues of a zinc chloride flux used in soldering may also have proved toxic. For several days a white sediment appeared at the bottom of each cage in use.

Large and small cages were installed in each of 16 pools, distributed among the three main vegetational types of habitat: open spruce and larch forest,

tundra, and scrub willow and birch. The locations of these pools are indicated on the map (Fig. 11), and the information obtained from them is summarized in Tables I, II, III, and IV. A brief description of each pool follows, and typical pools from each habitat are illustrated in Figs. 1 to 6.

Open Spruce–Larch Forest (*Five Stations*)

Station A.—This was a deep medium-sized pool in open forest (Fig. 2), with muck bottom and grassy margins, and heavily discolored water; *Hippuris vulgaris* grew in the pool. The surrounding ground flora consisted of mosses, *Eriophorum*, *Carex*, *Petasites*, *Vaccinium uliginosum*, and *Ledum groenlandicum*. On May 31, first- and second-instar larvae were present in moderate numbers in the grassy margins, and by June 5 these had reached the fourth instar. Rapid drying up of the grassy parts of the pool about July 8 killed the larvae, which were still in the fourth instar.

Station E.—This was a moderately large pool in light forest; it was about 6 in. deep, with a grassy bottom; in the vicinity were hummocks with abundant moss and lichen. First- and second-instar larvae continued to appear in this pool until June 10, when the last of the snow around it melted. *A. excrucians* reached the fourth instar by June 25, and peak numbers of pupae occurred on July 5.

Station N.—This was a large, rather deep pool with a bottom of decaying willow leaves; it was in a burnt-over, and hence rather open, forest area, with a ground flora of mosses, grasses, and *Carex*, *Ledum*, *Polytrichum*, and some willow. This station was established on June 15, when large numbers of larvae and pupae were present. By June 23 many adults had emerged, predominantly males; by June 27 over 200 females had emerged.

Station O.—This was a large, well defined forest pool (Fig. 1), with steep banks covered with mosses and ericaceous plants, and the bottom of soft black muck, the water yellowish. The ground flora was abundant, but grasses and sedges were scant. This station was established on June 15, when larvae of *A. communis* were present in the second to fourth instars. Pupation was almost complete by June 27.

Station P.—This pool is described under the heading of forest pools, since the original vegetation and most of the surrounding area was forest. The area had been burnt over and was largely open, with considerable growth of birch and willow. The bottoms of all pools in this locality were of soft black muck with a yellow surface. No cage was used here.

Tundra (*Six Stations*)

Station C.—This was a medium-sized pool in rather grassy tundra; scattered larch, birch, and willow occurred in the vicinity, and the abundant ground flora included *Ledum*, *Vaccinium*, *Pinguicula*, *Pedicularis*, *Andromeda*, *Rubus*, and *Pyrola* species. On June 1, third- and fourth-instar larvae of several species were very abundant. Pupation was almost completed by June 23, and peak emergence occurred about June 26. Drying up of the pool resulted in heavy mortality.

Station D.—This was a medium-sized pool about 6 in. deep, with a mixture of muck and grassy bottom, and long grass and sedges around the margin; some dwarf birch, larch, and spruce were in the vicinity. First- and second-instar larvae were present on May 31; fourth-instar larvae occurred by June 5, peak numbers of pupae about June 29, and the first emergence on June 26.

Station F.—This was a shallow pool in open *Carex* tundra (Fig. 3) with a bottom of yellow muck and decaying lichen, and abundant *Andromeda* and *Rhododendron* on surrounding hummocks; *Pedicularis*, *Ledum*, *Pinguicula*, and *Vaccinium* were also common. On June 2, third- and fourth-stage larvae were found in small numbers. Pupae reached a peak by June 21, and maximum emergence occurred on June 25. The pool dried up by July 8.

Station G.—This was a flooded area, which dwindled to a collection of pools similar to that at Station F, but with some spruce in the vicinity. Second- and third-instar larvae were present on June 2; pupae reached a peak on June 26, and maximum emergence occurred about June 28. This area dried up rapidly early in July.

Station H.—This was a long, narrow, permanent pool about 6 in. deep (Fig. 4), rather close to open forest. *Carex* was abundant in the bottom and margins, and some algae occurred on the surface; *Rhododendron*, *Andromeda*, and *Vaccinium* were in the immediate vicinity. There was a moderate number of fourth-instar larvae on June 2; the first pupae appeared on June 4, and emergence was at its peak by June 21. This pool, which did not dry up, produced a high proportion of adults infested by larval hydrachnid mites; some individuals, with 20 or more of these mites attached to them, were found dead, lying on the surface of the water. This is of particular interest in view of the recent observations that such mites affect oviposition of *Aedes trivittatus* (2).

Station J.—This was a rather small, shallow, temporary pool, with a yellow muck bottom, and sedges, grasses, and some moss and lichens around the margins. Third- and fourth-stage larvae were present on June 3; these had reached the pupal stage by June 8, and most had emerged by June 25.

Scrub Willow and Birch (Five Stations)

Station B.—This was a small temporary pool, 6 to 8 in. deep, on the flood plain of the Churchill River. The bottom was of yellow muck and grasses, and the surrounding ground flora consisted of grasses, *Carex*, and *Potentilla*. It was one of the smallest pools used, and temperature changes were extreme. The water temperature went up to 80° F. on June 1 and down to 44° F. on June 12. Pupae were first recorded here on June 14, and adults emerged on June 21.

Station I.—This was a small pool with a muck bottom and grassy margins, near the high-tide mark of the Churchill River estuary. DDT was deposited here at rather less than 0.1 lb. per acre from an aerosol in June, 1947. The depth was about four inches. *Poa and Potentilla* grew around the pool, and *Triglochin maritima* in it. The larval population was rather small; first and

second instars were present on June 3. Fourth-instar larvae were recorded on June 14, pupae on June 21, and the first emergence on June 28. The pool dried up early in July.

Station K.—This was a small, shallow, temporary pool (Fig. 5) on the flood plain of the Churchill River. The bottom was heavily grown with grasses and sedges, and *Rumex* and *Petasites* grew around the margins. Third-instar larvae were present on June 7, pupae occurred on June 21, and adults emerged on June 25.

Station L.—This was a larger and deeper pool than Station K, but otherwise similar in character, location, and vegetation. Larvae had reached the fourth instar by June 10, but none pupated until June 24. Emergence, however, was rapid and almost complete by June 28.

Station M.—This was a small temporary pool (Fig. 6), similar to Stations K and L, but rather larger. Larvae in all stages were present on June 7, pupae occurred by June 18, and adults had emerged by June 23.

In spite of the transitional nature of the vegetation around many of the stations, the last three columns of Table IV show *A. communis* to be a true forest species, with *A. punctor* resembling it in this respect. *A. nigripes* is the species most clearly associated with tundra areas, and *A. nearcticus* shows a similar tendency.

TABLE IV

SUMMARY OF DATA FROM INSECTARY REARING OF MATERIAL FROM FIELD STATIONS

Species	Range of emergence dates	Duration of pupal period in days:		Total No. specimens reared from:		No. of stations in each type of habitat		
		Range	Mean	Larvae	Pupae	Open forest	Tundra	Birch–willow scrub
A. nearcticus	June 15–26	5–12	7.8	56	3	1	3	3
A. nigripes	June 18–29	3–12	6.3	41	10	0	5	2
A. punctor	June 17–July 8	2–16	7.7	34	13	3	3	2
A. communis	June 21–30	3–8	6.1	18	3	5	2	0
A. excrucians	June 30–July 19	3–10	5.1	48	19	2	2	1
A. campestris	June 30–July 23	2–7	4.8	29	0	1	0	1
A. flavescens	July 5–9	5–7	6.1	8	0	0	0	1
A. riparius	June 30	>3	>3	0	1	0	1	0
Mochlonyx culiciformis	June 30–July 13	4–6	4.9	17	7	1	1	0

The range of emergence dates for each sex and for each species, as obtained from these field cages, is indicated in Fig. 13, on which degree-days above 32° F. are also plotted. In every species the first males emerged from one to five days earlier than the first females, and the last females from one to 15 days later than the last males. The species have been arranged in an order that is considered to represent the degree of adaptation to conditions in high latitudes, with low temperatures and short summers. With the exception of *A. communis*, for which the data are insufficient, there is a steadily increasing

spread of emergence with increasing number of degree-days* to the first emergence. Observations on mating habits, discussed later, suggest that *A. communis* continued to emerge until at least July 13.

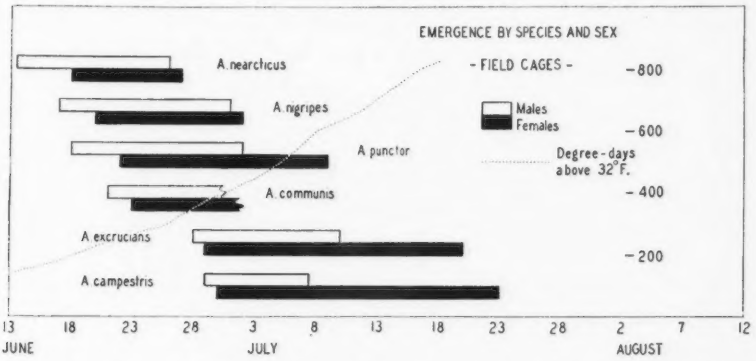


FIG. 13. *The dates of field emergence of mosquito species, males and females, in relation to degree-days above 32° F.*

The data from field cages also suggest that the sex ratio for these species is initially about 1 : 1; early drying up of pools, however, results in cutting off more of the later-maturing females than of the males. This results in a temporary surplus of males, a situation that is soon reversed by the earlier deaths of males.

Insectary Rearing

Representative collections of larvae and pupae from each field station and from other sites were brought in for rearing in the insectary (Fig. 10). A number of larvae from each batch were killed, identified, and preserved, to give some preliminary indication of the species present in the different habitats. The remainder were raised in pint sealers half-filled with water. The water in the sealers was changed about every four days, being replaced with that from mosquito-breeding pools near the insectary. Food materials came from the same pools, and were brought in usually on grasses or mosses.

Larvae isolated in the insectary for individual rearing, to associate the last larval exuvium with the adult, were invariably slower in maturing than comparable larvae that were reared together under otherwise identical conditions.

When a larva pupated, the pupa was isolated in another pint sealer, and an individual rearing record was maintained. When the pupa was isolated, the larval skin was removed, preserved, and labelled to enable it to be associated with the ultimate adult. The jars were cleared of pupae twice daily, once in the morning and again in the late afternoon or evening. Thus individual larval skins were associated with the appropriate adults.

* *Obtained by subtracting 32 from the daily mean temperature and adding the results in sequence throughout the season.*

Jars in which pupae were kept were about 8/10 filled with water. A few small pieces of cork were cut and placed on the surface of the water, and three or four long pieces of dry grasses were added so that they projected above the surface of the water. A glass lamp globe, covered at one end with cheesecloth, was placed over the mouth of the jar. It was not found necessary to change the water in the pupal jars, which were kept in a dark place and handled as little as possible.

The jars containing pupae were cleared of emerged adults twice daily. This usually allowed the newly-emerged adults a few hours in which to harden before they were killed and pinned. Each last larval skin was mounted in euparal on a small strip of celluloid. Where there was no doubt in linking last larval skin and adult, the mounted skin was pinned directly below the adult. Where more than one skin was associated with the specimen, these multiple skins were pinned together, and identified by a label giving the numbers of the adult specimens with which they were linked.

Morning and evening readings of maximum and minimum temperature and of relative humidity, both inside and outside the insectary, were taken throughout the rearing period. The information obtained from insectary records concerning the distribution of species among the pool types is summarized in Tables I, II, III, and IV.

Studies of Adult Mosquitoes

Seasonal Changes in the Population

From June 24 to Aug. 14 a survey was carried out of the activities of adult mosquitoes. The main objectives were to determine the succession of species and the relationship of meteorological conditions to flying and biting activity.

Two quantities, the 'landing rate' and the 'biting rate', were used as indices of mosquito attack. The landing rate was taken as the number of adults alighting per minute on the trousers' front between the knees and hips of the observer while facing in a direction halfway between down wind and toward the sun, and the biting rate was taken as the number of bites per minute on the forearm, from wrist to elbow, the bare forearm being held in the shelter of the body. The same subject was used throughout for obtaining these data.

The abundance of adult mosquitoes on the wing was estimated by counting the numbers captured by 20 full sweeps in both directions with a large net, immediately on arriving at a station.

The computation of averages for five consecutive days of biting rate, landing rate, and population on the wing, for all observation stations collectively, virtually eliminates minor fluctuations due to differences of weather and terrain. If a curve for landing rate is drawn from these figures on a reduced scale of 5 : 1, it corresponds very closely with a biting rate curve; these two sets of figures have therefore been combined. The resulting data are plotted in Fig. 14, and give a useful picture of the normal trends in population and activity. Each of the curves shows three maxima, not one as has been hitherto

supposed. The peaks of population on the wing fall on June 30, July 9, and July 15. The numbers of females of various species-groups emerging during this period, plotted below the graph in Fig. 14, indicate clearly that the first of these peaks represents mainly the tundra black-legged species, *A. nearcticus* and *A. nigripes*, and the second represents the residue of this population plus

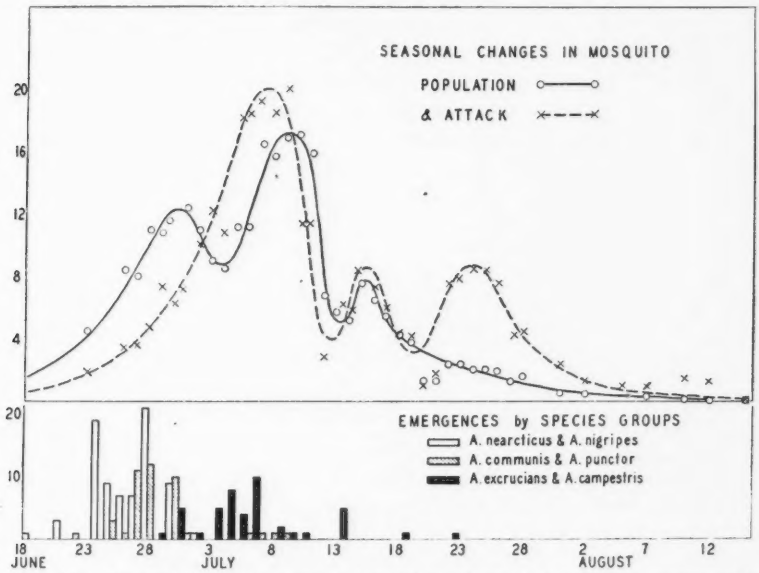


FIG. 14. *Seasonal changes in mosquito population and attack in relation to emergences by species groups.*

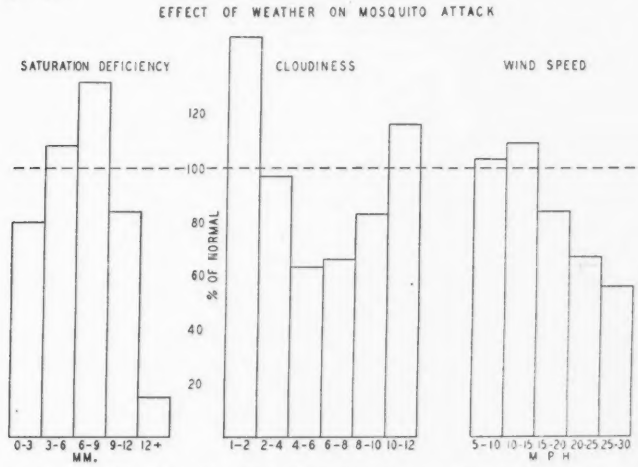


FIG. 15. *The effect of weather on mosquito attack.*

the peak population of the woodland black-legged species, *A. punctor* and *A. communis*. Finally, the third peak arises when *A. excrucians*, *A. campestris*, and *A. flavescens*, the banded-legged species, are added to the now dwindling population of the black-legged species. Furthermore, it may be seen that full flight activity of the tundra species follows very promptly on emergence, whereas that of the forest species is delayed nearly a week, and that of the banded-legged species for two or three days.

The peaks of the composite curve of attack fall on July 7, 15, and 24, indicating that on the average the tundra black-legged mosquitoes are most inclined to bite man seven days after emergence; whereas the greatest inclination to bite on the part of the four remaining species comes 10 to 11 days after emergence. Both of these intervals are longer than has been generally supposed. These results are an interesting confirmation of the deductions from Fig. 13: the close adaptation of *A. nigripes* and especially of *A. nearcticus* to the short northern summer, as compared with *A. punctor* and *A. communis*, and even more so with the banded-legged species. In comparison with the population peak, the biting rate peak is higher for the tundra black-legged species than for the remaining species, suggesting a greater persistence in attack on the part of the former.

If the rather inadequate data obtained in 1947 on this subject are re-examined in the light of these results, a second peak of biting rate is discernible here also. The approximate peak dates in 1947 were July 9 and July 15 (17).

This survey throughout the season was supplemented by two detailed 24 hr. surveys: one on July 12–13, on the tundra at the site used in 1947 (17), and one on July 16–17, in the forest at Warkworth Creek. Some of the data from these surveys are presented in graphical form in Figs. 16 and 17. In these graphs the black columns represent mosquito attack, computed from biting rate and landing rate figures. Open columns represent the proportion of the sky covered by cloud, and the broken and solid lines represent temperature and saturation deficiency respectively. The heavy line at the top of each graph represents the hours of darkness; records began between 10 and 11 a.m.

The graph for the tundra species shows remarkably close correlation between cloudiness and mosquito attack, a fact that has been previously observed by Hunter (6). There was a rough peak of activity shortly after nightfall, when both temperature and saturation deficiency were falling rapidly. In the forest graph, as would be expected, the correlation with cloudiness is less well marked, and there were two well-defined peaks of attack, one shortly before sundown, and a second shortly after sunrise. The influence of saturation deficiency appears to be delayed, attack figures rising shortly after a fall in saturation deficiency, and falling shortly after a rise. It is noteworthy that rather high biting rates were recorded at temperatures below 7° C. (45° F.); Mellanby (12) records the flight threshold of *A. punctor*, a dominant species in this collection, as about 10° C. (50° F.) in Lapland. Wind speed throughout both of these 24 hr. periods was low, and the figures show no pronounced effect on attack owing to changes in this factor or in light intensity. These

data do not support the statement of Matheson (11, p. 44) that all our far northern *Aedes* species are primarily diurnal. Further data are required

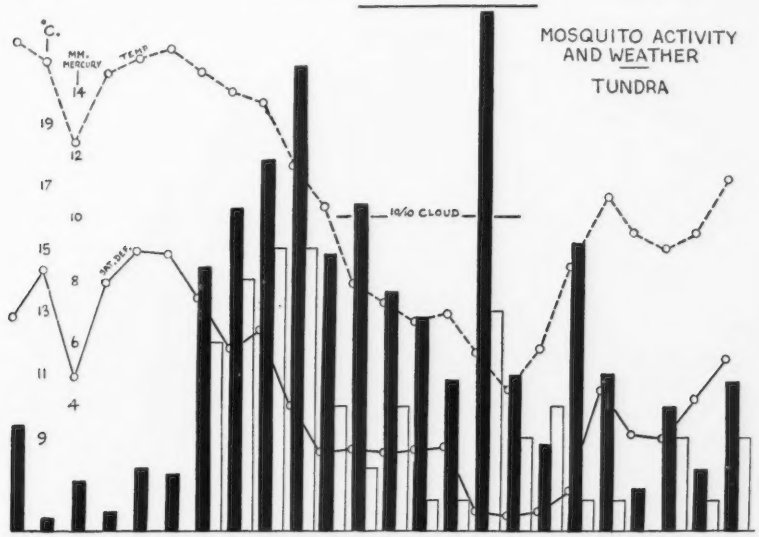


FIG. 16. *Daily changes in mosquito activity and weather at a tundra location. Explanation on p. 72.*

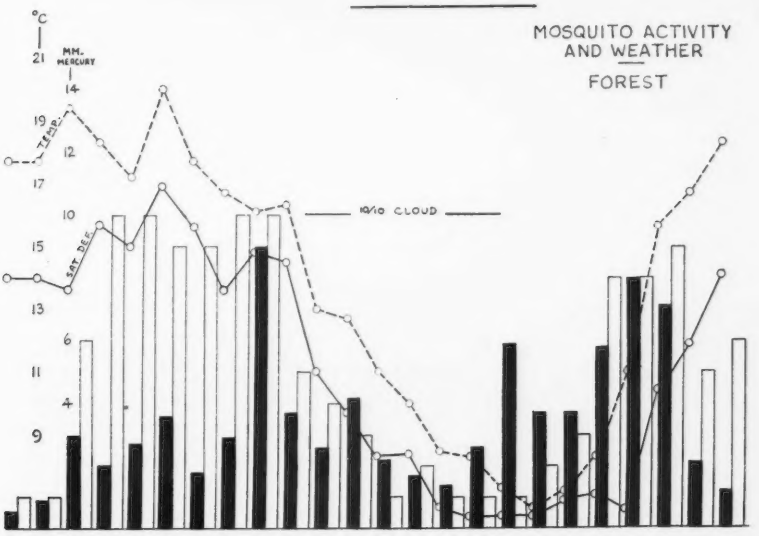


FIG. 17. *Daily changes in mosquito activity and weather at a forest location. Explanation on p. 72.*

before specific variation in activity can be expected to show up, but an examination of the material taken at these collections confirms the impression obtained in 1947 that *A. cinereus* is restricted in its biting activity to a few hours before sunset, and again after sunrise.

The Effects of Weather on Activity

The effects of weather factors on activity were evaluated on the basis of the curve in Fig. 14, in which the effects of daily weather changes have been levelled out, and which may be said to represent the normal sequence of activity throughout the season.

The actual attack figures for each day, taking all observations collectively and averaging them, were expressed as a percentage of the normal for that day, as indicated by the curve. The following weather factors were then investigated: temperature, barometric pressure, wind speed and wind direction, saturation deficiency, cloudiness, and hours of sunshine. For each factor, the mean value during the period of observations on each day was used; the recorded range of these mean values was divided into five or six equal blocks as shown in Fig. 15. The percentages of the normal attack, for all days during the season when the value of any particular weather factor fell within a certain block, were averaged. These averages are recorded in the diagram in Fig. 15, for saturation deficiency, cloudiness,* and wind speed. No other weather factor gave results indicating that it had any great influence on mosquito attack.

Between temperatures of 50° and 80° F. there is no regular variation in attack; data beyond these limits are too meager for definite conclusions, but they suggest that the intensity of attack falls off rapidly at both higher and lower temperatures. The data for barometric pressure suggest that there is some diminution in attack at very high pressures, but this is inconclusive. The relationship of attack with hours of sunshine agrees closely with the inverse of that illustrated for cloudiness, except that very high figures for sunlight do not give so great an increase in attack as do very low figures for cloudiness. Though strong onshore winds would be expected to result in a somewhat delayed reduction in attack, and offshore winds to result in a corresponding increase, neither of these effects could be demonstrated from the figures available.

There is, of course, some inverse correlation between saturation deficiency and cloudiness, so that these two diagrams corroborate each other. Cloudiness, however, also influences light intensity, although the 24-hr. studies suggest that light intensity has no great influence on attack. The well known intensity of mosquito attack immediately prior to thunderstorms can be explained as the combined effect of the three important factors here: low wind speed, cloudiness, and low saturation deficiency.

** The numbers below the base line of the "cloudiness" diagram are arbitrary. A numerical value was allocated to each of the expressions used in the meteorological sheets (clear, overcast, etc.) and these were added for the period of observation. For example, the highest number, 12, means completely overcast throughout the period of observation, whereas the number 6 indicates either completely overcast for half the period, or 5/10 cloudy for the whole period.*

The procedure used in studying the influence of weather factors on attack was also applied to a study of the influence of the same factors on flying activity, on the basis of the solid curve in Fig. 14. Although there is a suggestion of the same effects on flight as on attack for both cloudiness and saturation deficiency, the only clearly shown relationship is that of wind speed.

The influence of wind speed, both on flying and on biting activity, appears to be primarily a mechanical one: because controlled flight in the wind is difficult, biting is also difficult. However, by increasing evaporation, higher wind speeds may also influence mosquitoes in the same way as high saturation deficiencies. It is known that many mosquito species are unable to digest a blood meal without access to water, and this has been suggested for some at least of the species considered here (3). The most striking reduction in mosquito attack occurs with high saturation deficiency, presumably for this reason. It thus appears that the same drying conditions that limit the numbers of mosquito larvae reaching maturity are also of great importance in limiting the ability of the adults to seek out and utilize the blood meal apparently required for the production of abundant eggs.

Mating

The first interest of the newly emerged adult of all Churchill species of *Aedes* appears to be mating, which takes place shortly after emergence, at least in the tundra species. The typical mosquito mating swarm has now been observed for most of these species; observations on *A. nigripes* and *A. punctor* have already been recorded (17); further observations are given here:

On July 16, at Warkworth Creek, *A. punctor*, together with *A. communis*, formed one enormous swarm over the Hudson Bay Railway track, appearing as a dark cloud stretching as far as the eye could see, and extending round the bend of the track. This swarm persisted from 8.30 p.m. until 9.00 p.m., all individuals heading in the same direction at any one time, sometimes north and sometimes south, but always along the railway track, and at a height of 3 to 10 feet above the ground. There was no wind during this time; the air temperature over the track was 62° F., that over the vegetation on either side 58° F.; saturation deficiency decreased from 4.3 to 3.7 mm. of mercury, and light intensity remained at about 650 lumens per square foot. Cloud was 4/10 and the sun set at 9.45 p.m.

At 8.30 p.m. on the same evening, rather small swarms of *A. campestris* were seen over a forest clearing at Warkworth Creek, at a height of 6 to 12 ft.

On July 12, *A. excrucians* was observed swarming over open tundra at 9.30 p.m. The temperature was 61° F., saturation deficiency 2.5 mm., wind speed 5 m.p.h., and light intensity 90 lumens per sq. ft. A swarm was also noted in a clearing in light forest with a floor of sedges and some moss and lichen. The average height of the swarm was about 14 ft. The dancing movements appeared to consist of the formation of a compact cluster at the upper extremity of the swarm, the cluster lasting from two to five seconds, then breaking and re-forming at a somewhat different level.

Further evidence of the remarkable sensitivity to temperature indicated in these notes was obtained two hours after sunrise on July 17, when mosquitoes and black flies were seen to select as resting sites the charred vertical surfaces of tree stumps in a burnt-off area. The temperature of these surfaces was found to average two Fahrenheit degrees higher than that of living tree trunks.

Feeding and Oviposition

Mosquitoes having mated, man has no longer any practical interest in the male mosquito, but becomes as interested in the female as she in him. The well-established fact that many mosquito species can lay viable eggs without having a blood meal, although the number may be reduced, may be true of Churchill species. Certainly, as the season progresses, the majority of the mosquitoes that are attracted to man carry eggs in various stages of development, although it seems questionable that many of them have fed on blood. A list of birds and mammals seen in the area is given as an appendix; of the mammals, the most commonly seen during the fly season are the white whale, and mice and lemmings. Nestling birds, and amphibia, have been watched, but mosquitoes were not seen to feed on these, possibly because the observer was preferred. Natvig (13) has recorded various species attacking nestling birds in Norway, including *A. punctor* on the sparrow hawk, *A. communis* on grouse, and *A. excrucians* and *A. intrudens* on the golden eagle. Other nestling birds reported attacked, but for which no specimens were identified, included the rough-legged buzzard, rook, crow, gull, lapwing, and kestrel. Longstaff (7) has reported *A. nigripes* feeding on the redpoll and perhaps the arctic hare in Greenland, and Thienemann (15) records *A. punctor* and *A. communis* apparently feeding on *Microtus* and lemmings. Figs. 7 and 8 illustrate stages in the feeding of *A. nearcticus* on man; the sagging of the abdomen in the second stage is striking.

Feeding on nectar appears to be a universal habit among the females of Churchill species of mosquito, and here, circumstantial evidence has been kind. The very common woodland orchid, *Habenaria obtusata* Pursh., as previously reported by Raup (14), is apparently normally pollinated by mosquitoes, which, when visiting mature flowers, presumably for nectar, pick up one or both of the pollinia, the latter adhering to the ventral margins of the eyes. At Churchill, on July 24, and 25, 1947, 6% of mosquitoes were found to be carrying the pollinia of this orchid (17). A larger sample collected on July 12, 13, 16, and 17, 1948, gave the following figures: total mosquitoes, 1364; number carrying a single pollinium, 55; number carrying two pollinia, 3. It seems reasonable to assume that the probability of a mosquito picking up the left pollinium when feeding on *Habenaria* is the same as the probability of picking up the right pollinium; and in fact the numbers with right and left pollinia are roughly equal. The probability of picking up both pollinia is then the square of the probability of picking up one; and the ratio of the number with two pollinia to the number with one is the same as the ratio of the number with one to the number that has visited the orchid. On these assumptions,

no fewer than 74% of the mosquitoes attracted to man at the middle of July, 1948, had fed on *Habenaria obtusata*. In 1949 a much larger sample, taken earlier in the season, indicated that 28% had fed on this orchid (3). Figures for all three years are in no way conflicting, since they indicate that more mosquitoes fed on the orchid as the season progressed.

These are remarkably high figures, when it is considered that numerous other flowers that are accessible to mosquitoes at this time secrete nectar. Among these may be mentioned *Rhododendron lapponicum* L., *Ledum palustre* L., and *Dryas integrifolia* Vahl., all of which are extremely abundant, and on all of which mosquitoes have been observed resting and apparently feeding. Pollinia of *H. obtusata* have been found on all the species of *Aedes* at Churchill. On two occasions mosquitoes have been observed feeding on *Habenaria hyperborea* L.; and Fig. 9, paid for with no small amount of blood, shows *A. punctor* preparing to feed on this species. However, neither the pollinia of this, nor those of other common species of orchid, have been found attached to mosquitoes.

Captive mosquitoes of various species fed readily on sugar solutions of a wide range of concentration in the laboratory. The process of feeding, however, was much slower than feeding on blood, and the quantity of solution consumed at a single meal never approached that of the normal blood meal.

No observations were made on oviposition in the field. In most individuals of all species collected on July 17, development of the eggs had scarcely begun; in one specimen of *A. campestris* eggs could be detected, and in one of *A. communis* (?) about 50 developing eggs could be counted in each ovary. Further dissections on July 26 revealed considerable progress in development, although eggs were still far from ready to be laid. A total of 170 eggs could be counted in specimens of *A. punctor* and 300 in *A. excrucians*.

Captive specimens of *A. campestris*, given a blood meal and provided with soaked raisins in the insectary on July 12, laid eggs on wet cotton on July 27 and 28. Although given no more food, they lived for a considerable time, the last ones dying on Aug. 11. Two of these were dissected and were found to contain 104 and 166 eggs respectively. Dissections of collected *A. excrucians* on July 28 showed only one specimen with eggs well enough developed to count; the eggs numbered 130. Ten specimens of *A. excrucians* were caged on July 28 and were fed blood meals. All had died without laying eggs by Aug. 11; one of these was dissected and contained 203 eggs. Five more specimens of *A. excrucians* were caged on Aug. 11 and were given blood meals on Aug. 12. These also died without laying eggs. Two of them were dissected, and had 254 and 213 eggs respectively.

Acknowledgments

Grateful acknowledgment is made of valued contributions of the following: W. C. McDuffie,* who was in charge of the United States group at Churchill,

* *U.S.D.A., Agr. Research Adm., Bureau of Entomology and Plant Quarantine, Kerrville, Texas.*

J. F. Sharp,** and R. W. Fisher,** who assisted in organizing and carrying out the field studies, R. P. Thompson,*** who was in charge of the insectary rearings; W. E. Beckel,** who identified mosquito specimens; J. M. Gillett,† who identified plant specimens, and Dr. A. W. A. Brown,†† who gave advice and assistance in the initial stages of the project.

References

1. Abdel-Malek, A. Plant hormones as a factor in the hatching of *A. trivittatus* eggs. Ann. Entomol. Soc. Am. 41 : 51-57. 1948.
2. Abdel-Malek, A. The biology of *Aedes trivittatus*. J. Econ. Entomol. 41 : 951-954. 1948.
3. Davies, G. R. Unpublished communication. 1949.
4. Goldsmith, J. B., Husman, C. N., Brown, A. W. A., and Sharp, J. F. Exploratory studies on the control of adult mosquitoes and black flies with DDT under arctic conditions. Mosquito News, 9 : 93-97. 1949.
5. Hocking, B., Twinn, C. R., and McDuffie, Wm. C. A preliminary evaluation of some insecticides against immature stages of black flies (Diptera: Simuliidae). Sci. Agr. 29 : 69-80. 1949.
6. Hunter, W. D. An unusual invasion of *Aedes sollicitans* in Louisiana. J. Econ. Entomol. 3 : 504. 1910.
7. Longstaff, T. G. An ecological reconnaissance in west Greenland. J. Animal Ecol. 1 : 119-142. 1932.
8. McClure, H. E. Aspection in the biotic communities of the Churchill area, Manitoba. Ecol. Monographs, 13 : 3-35. 1943.
9. McDuffie, Wm. C., Cross, H. F., Twinn, C. R., Brown, A. W. A., and Husman, C. N. The effectiveness of DDT and other insecticides as larvicides against arctic species of *Aedes*. Mosquito News, 9 : 145-149. 1949.
10. McDuffie, Wm. C., Sharp, J. F., Cross, H. F., Twinn, C. R., and Wilson, D. M. The effectiveness of prehatching treatments for the control of arctic mosquitoes. Mosquito News, 9 : 51-56. 1949.
11. Matheson, R. Handbook of the mosquitoes of North America. 2nd ed. Comstock Publishing Co., Inc., Ithaca, N.Y. 1944.
12. Mellanby, K. The activity of certain arctic insects at low temperatures. J. Animal Ecol. 9 : 296-301. 1940.
13. Natvig, L. R. Contributions to the knowledge of the Danish and Fennoscandian mosquitoes. Culicini. Norsk Entomologisk Tidsskrift. Suppl. I, Oslo: A. W. Broggers Boktrykkeri A/S. 1948.
14. Raup, H. M. The pollinization of *Habenaria obtusata*. Rhodora, 32 : 88-89. 1930.
15. Thienemann, A. Die Stechmückenplage im hohen Norden. *Abstracted in* Rev. Applied Entomol., B, 27 : 128. 1939.
16. Twinn, C. R. Studies of the biology and control of biting flies in northern Canada. Arctic Journal. In press.
17. Twinn, C. R., Hocking, B., McDuffie, Wm. C., and Cross, H. F. A preliminary account of the biting flies at Churchill, Manitoba. Can. J. Research, D, 26 : 334-357. 1948.

** *Division of Entomology, Science Service, Department of Agriculture, Ottawa, Canada.*
*** *Defence Research Board, Ottawa, Canada.*
† *Division of Botany, Science Service, Department of Agriculture, Ottawa, Canada.*
†† *Professor of Zoology and Applied Biology, University of Western Ontario, London, Ont.*

Appendix

Sight records of birds and mammals during the fly season at Churchill.*

Birds:

Gaviidae
- Common loon, *Gavia immer*

Ardeidae
- American bittern, *Botaurus lentiginosus*

Anatidae
- Canada goose, *Branta canadensis*
- Pintail, *Anas acuta tzitzihoa*
- Lesser scaup duck, *Aythya affinis*
- American golden eye, *Glaucionetta clangula*
- Red-breasted merganser, *Mergus serrator*

Accipitridae
- Rough-legged hawk, *Buteo lagopus*

Tetraonidae
- Willow ptarmigan, *Lagopus lagopus*

Charadriidae
- Semipalmated plover, *Charadrius hiaticula semipalmatus*
- Golden plover, *Pluvialis dominica dominica*

Scolopacidae
- Hudsonian curlew, *Numenius phaeopus hudsonicus*
- Hudsonian godwit, *Limosa haemastica*
- Wilson's snipe, *Capella gallinago delicata*
- Lesser yellow legs, *Totanus flavipes*
- Least sandpiper, *Erolia minutilla*
- Semipalmated sandpiper, *Ereunetes pusillus*
- Stilt sandpiper, *Micropalama himantopus*

Phalaropodidae
- Northern phalarope, *Lobipes lobatus*
- Red phalarope, *Phalaropus fulicarius*

Stercorariidae
- Parasitic jaeger, *Stercorarius parasiticus*

Laridae
- Herring gull, *Larus argentatus*
- Glaucous gull, *Larus hyperboreus*
- Arctic tern, *Sterna paradisaea*

Strigidae
- Snowy owl, *Nyctea scandiaca*
- Short-eared owl, *Asio flammeus*

** The list of birds was checked by W. Earl Godfrey and the list of mammals by Austin W. Cameron, of the Zoological Division, National Museum, Ottawa, Canada.*

Birds—*Concluded:*

Alaudidae
Horned lark, *Eremophila alpestris*

Corvidae
Canada jay, *Perisoreus canadensis*
Crow, *Corvus brachyrhynchos*

Turdidae
Robin, *Turdus migratorius*

Laniidae
Northern shrike, *Lanius excubitor borealis*

Fringillidae
Snow bunting, *Plectrophenax nivalis nivalis*
White-crowned sparrow, *Zonotrichia leucophrys*
Eastern tree sparrow, *Spizella arborea arborea*
Pine grosbeak, *Pinicola enucleator leucura*
Lapland longspur, *Calcarius lapponicus lapponicus*

Mammals:

Rodentia
Porcupine, *Erethizon dorsatum*
Muskrat, *Ondatra zibethica*
Collared lemming, *Dicrostonyx groenlandicus richardsoni*
Muskeg meadow mouse, *Microtus pennsylvanicus drummondi*

Lagomorpha
Varying hare, *Lepus americanus*

Artiodactyla
Caribou, *Rangifer caribou*

Cetacea
White whale, *Delphinapterus leucas*

LARVAE OF DIPTEROUS PARASITES OF NYMPHAL AND ADULT GRASSHOPPERS[1]

R. W. SMITH[2] AND THELMA U. FINLAYSON[2]

Abstract

The first-instar larvae of 19 sarcophagid and one anthomyiid, and the second-instar larvae of four tachinid species parasitic in nymphal and adult grasshoppers in Canada are described in detail and keys presented for their identification.

Introduction

One requisite of any critical study of parasite incidence is a sufficient knowledge of the species involved to ensure their recognition. Any study of parasitism of nymphal and adult grasshoppers requires an acquaintance with many species of grasshoppers and several families of Diptera and Hymenoptera and preferably some acquaintance with the family Mermithidae. Among the grasshopper parasites, the Diptera form the largest and probably the most important group.

Keys for the identification of adult Diptera likely to be encountered as parasites of grasshoppers in Canada are available in the literature (1, 6, 14, 16, 28, 35); however, in the Sarcophagidae it is frequently necessary to have males for specific determinations. Few descriptions (12, 13, 21) are available for the identification of grasshopper parasites in their immature stages. If, however, they are to be recognized as they occur within their hosts they must be distinguished in these stages.

This paper does not include all the dipterous parasites found in grasshoppers in Canada, but does include those that have occurred most frequently in current investigations in parts of the Prairie Provinces and British Columbia, and at one point near Belleville, Ont. Southern Manitoba has been surveyed most extensively, especially the Red River Valley and the southwestern area. Saskatchewan material has been collected at widely separated points from Saskatoon to the southern border of the province, and in Alberta collections have been made near Carmangay and Drumheller. In British Columbia more limited collections were obtained from the Nicola and Lac du Bois ranges near Kamloops. In Ontario, the seasonal occurrence of parasites has been closely watched and recorded at Chatterton, near Belleville. A few collections, for rearing, have also been taken from points in Quebec, Prince Edward Island, New Brunswick, and Ontario.

Particular attention has been given to parasites of *Melanoplus bivittatus* (Say), *M. mexicanus mexicanus* (Sauss.), and *Camnula pellucida* (Scudd.), although more than 20 different species of grasshoppers have been examined

[1] *Manuscript received October 12, 1949.*

Contribution No. 2616, Division of Entomology, Science Service, Department of Agriculture, Ottawa, Canada.

[2] *Dominion Parasite Laboratory, Belleville, Ont.*

for parasites. The parasites are those found in all stages of the hosts from the first nymphal instar to the adult, and occur in the field from mid-May to mid-September or later. Many of the immature stages of the parasites encountered are now sufficiently well known to be recognized to species.

In addition to the larvae of dipterous parasites the only parasites found in grasshoppers in any numbers were the threadlike Mermithidae (Nematoda) and the planidia of the secondary parasite, *Perilampus hyalinus* Say (Hymenoptera).

The investigations of parasitism of grasshoppers in Canada are being carried on co-operatively by the Units of Biological Control Investigations and Field Crop Insect Investigations of the Division of Entomology.

Material and Methods

Immature stages of the parasites were obtained from hosts and gravid females collected in the field or taken from laboratory-propagated stock. Field collections have provided the greatest amount of material for examination and have been the only source of larvae of species not yet propagated in the laboratory. Most of this material, however, has been in preservative. Laboratory propagation, on the other hand, has provided living material and has been the means of definitely associating immature stages with male and female adults.

Propagation of the sarcophagids has been successfully carried out in the laboratory by placing first-stage larvae in hosts through the stub of an amputated fore- or mid-femur. The larvae are obtained by removing the abdomen from an etherized gravid female and placing the uterus with its larvae in a drop of water on a black slide. The larvae are then transferred to the grasshopper by means of a camel's-hair brush. The parasitized hosts are fed wheat blades, lettuce, or other food until the mature parasite larvae leave the host. The larvae are then allowed to pupate and transform to adults. Although the sarcophagids have been successfully reared in this manner, none of the tachinids has yet been propagated in the laboratory.

Detailed studies of the larval characters were made from specimens mounted on slides in Faure's solution.* In preparing a slide a touch of plasticine is first placed on each corner of a square (20.0 mm.) cover slip. The larva is then placed in a drop of Faure's solution on a 1 × 3 in. slide and the cover slip applied, plasticine side down. The cover slip is depressed carefully and the larva oriented to the desired position by manipulating the cover slip. Living first-stage larvae may be placed directly into Faure's solution without previous treatment, but in this case it is necessary to make sure that all movement has ceased before the mount is set aside to dry.

Specimens were examined with magnifications up to ×400 and the illustrations made with the aid of an ocular prism.

* *Gum arabic, 30 gm.; chloral hydrate, 50 gm.; glycerine, 20 cc.; distilled water, 50 cc.; cocaine hydrochloride, 0.5 gm.*

Specific identification of first-stage larvae was accomplished largely through laboratory propagation and subsequent association with adult males and females. In a few cases, linkages were deduced from the occurrence of particular larvae in the same or related collections of grasshoppers from which adults of certain species emerged. Gravid females, of course, provided a simple means of associating first-instar larvae with the female adult. Larvae not yet associated with their adult stages or associated with adults of undescribed species are tentatively designated by letter, such as *Sarcophaga* "C", and are not to be considered as similar to species so named by other authors. Proper trivial names will be given as soon as the larvae are linked with adults of described species.

Specific determinations of adults were either made or verified by the Systematic Unit, Division of Entomology, Dominion Department of Agriculture.

Larval Characters

With the exception of the Nemestrinidae all the larvae dealt with in the present study are typically muscoid in character. The nemestrinids are more elongate in form and differ in the type of the buccopharyngeal armature. Following the opinion of Keilin (19) and others (7, 27), the larvae are considered as consisting of a pseudocephalon, three thoracic and eight abdominal segments.

The pseudocephalon presents no characters of conspicuous specific value, although differences in the relative size of the antennae and position of the maxillary palpi do occur.

The extent, type, and arrangement of the spines on the thoracic and abdominal segments offer characters of specific and sometimes generic value. The segments may be completely or only partly encircled by spines; the spines may be large or small, elongate or short, straight or curved, and directed forward or backward. The spines are usually most abundant on the margins of the segments. In some species the intersegmental lines are poorly defined and the location of the spines cannot be determined with certainty.

The buccopharyngeal armature presents characters of prime importance for the separation and recognition of the different families, genera, and species. Along with the distribution and type of spines, the buccopharyngeal armature provides the most useful characters for the identification of species. The terminology used in describing this particular structure is in general that used by Keilin (19), Thompson (32, 33), and Snodgrass (27). A few additional terms employed by other writers have been adopted to simplify descriptions. For an explanation of the terms used, reference may be made to Figs. A to E. In the descriptions that follow, the mouth parts are considered as seen in profile.

The posterior spiracles and certain lobes on the last abdominal segment furnish further characters of value in the separation of the various groups. The spiracles of the Sarcophagidae are situated in a cavity on the posterior

surface of the segment and may be one- or two-lobed. Two clawlike appendages or processes are present on the lateral margins of the cavity in most, but not all, of this group of sarcophagids. These appendages have been reported by de Crouzel (7), who is of the opinion that they might serve to grasp the tracheae of the host into which the parasite inserts its own spiracles. Of the sarcophagids so far encountered only the genera *Protodexia* and *Kellymyia* lack these organs. The spine pattern on the floor of the posterior cavity also shows useful differences. On the posteroventral surface of the last abdominal segment, in the region of the anal opening, are frequently to be found four large lobes or swellings. The degree of development of these is occasionally of assistance in the identification of specimens.

In the Tachinidae the posterior spiracles are not in a cavity but appear on the surface as rather small, paired lobes, at the outer end of the felt chambers.

The posterior spiracles of the Nemestrinidae and Anthomyiidae differ considerably from those of the other parasites. The representatives of both these families have the spiracular slits arranged radially; those of the Nemestrinidae form a complete circle, those of *Acridomyia* an almost complete one.

Considerable growth takes place in the first larval stage, and since the larvae studied were in most cases of unknown age the measurements of size given in the descriptions of species must be considered as approximations.

The following key will serve to separate the various families in their larval stages.

Key to Families

1. Larva living free in the body cavity 3
   Larva with either integumental funnel or tube for contact with outside air 2
2. Respiratory attachment tubelike, convoluted, long; posterior spiracular slits arranged radially on circular plate; mouth parts not of muscoid type (p. 101) ... Nemestrinidae
   Respiratory attachment funnel-like, short; posterior spiracles protuberant, sometimes black; spiracle with button (3rd and 4th stages) ..... Tachinidae
3. Infrabuccal plate present, single median mandibular hook (Fig. D) (2nd stage, p. 98) .... Tachinidae
   Mouth parts without infrabuccal plate 4
4. Posterior spiracles widely spaced, slits arranged radially in almost complete circle 5
   Posterior spiracles in a cavity, slits not exceeding three in number and not forming almost complete circle 6
5. Mandibular hooks paired (2nd and 3rd stages) ..... Anthomyiidae
   Only one median mandibular hook (1st stage, p. 101) ..... Anthomyiidae
6. Posterior spiracles each with two or three separate slits; anterior spiracles present; dorsal wing of pharyngeal armature divided (2nd and 3rd stages) ..... Sarcophagidae
   Posterior spiracles single- or double-lobed; no anterior spiracles present; dorsal wing of pharyngeal armature not divided (1st stage, p. 84) .... Sarcophagidae

Sarcophagidae

In the present studies, the sarcophagids have exceeded in both number of species and number of individuals all other grasshopper parasites. This is so for Canada and apparently for other geographic regions as well (18, 22, 23, 25, 37).

The sarcophagids deposit living larvae or fully incubated eggs. These are placed on the host, the larvae eventually gaining entry through the more lightly sclerotized parts of the integument such as those around the bases of the legs and wings, or in the region of the occiput. The species that deposit larvae may place them on various parts of the body and, according to our own observations on parasites in cages and the observations of others, they may place them on hosts at rest or in the air. Those that deposit fully incubated eggs, such as *Protodexia* spp., usually place them in the folds between the abdominal segments or at the bases of the legs, while the host is on the ground.

All the larval stages are free-living within the body of the host. No evidence of attachment of larvae to the tracheae or air sacs of the host has been observed in the present study although the probability of such attachment has been suggested by de Crouzel (7).

A few published descriptions of sarcophagid larvae are of particular interest. Knipling (21), in his paper on the first-stage larvae of sarcophagids, describes the larvae of *Kellymyia kellyi* (Ald.) [= *Sarcophaga kellyi* Ald.] and *Helicobia rapax* (Wlk.) [= S. rapax Wlk.], two species that have been recorded as parasitic in grasshoppers. Knipling's *Sarcophaga* "A" is most certainly *Sarcophaga reversa* Ald., and his *Sarcophaga* "B" and "C" are larvae of the genus *Blaesoxiphotheca*, certain species of which are parasitic in grasshoppers. In the present investigation first-stage larvae of this genus have been most frequently found in the head of the host although their method of entry is not known.

de Crouzel (7) described in detail the first-stage larva of *Acridiophaga caridei* (Brèthes), a parasite of *Schistocerca paranensis* Burm. in South America. *A. caridei* has also been recorded as a parasite of grasshoppers in Western Canada (4). Descriptions of larvae of sarcophagid parasites of grasshoppers or locusts in other countries are to be found in papers by Olsaufiev (23) and Wood (37).

Key to First-stage Sarcophagid Larvae

1. Spines on pleural areas never approaching length of the mandibular sclerite.....2
   Spines on pleural areas as long as mandibular sclerites.....10
2. Oral hooks sickle- or beaklike in profile; spiracles two-lobed.....3
   Oral hooks leaf- or scalpel-like in profile; posterior spiracles single-lobed.....18
3. Infrahypostomal bridge apparently fused with the hypostomal sclerite (Fig. A).....4
   Infrahypostomal bridge articulated with hypostomal sclerite (Fig. B).....14
4. Only first five segments with spines on dorsal half, those on upper part of Segment 5 frequently restricted to a dorsolateral patch.....5
   More than five segments encircled with spines.....6
5. Mid-dorsal section of Segments 3 and 4 apparently without spines; spines on upper half of Segment 5 in dorsolateral patch only; spineless mid-dorsal section of Segment 5 equal in length to four or more times that of the longest spines of the lateral patch (Fig. 1).....*Sarcophaga reversa*
   Segment 5 encircled with spines except for mid-dorsal section which rarely exceeds length of longest spines in dorsolateral group; spines dense almost to mid-dorsal line on Segments 3 and 4 (Fig. 2).....*Sarcophaga* "H"
6. Only the six anterior segments encircled with spines (Fig. 3).....*Sarcophaga* "C"
   More than six anterior segments encircled with spines.....7

KEY TO FIRST-STAGE SARCOPHAGID LARVAE—*Concluded*

7. Only the seven anterior segments with encircling spines....8
   First eight anterior segments with encircling spines....9

8. Spines on anterior margin of Segment 2 moderately coarse and pricklelike (Fig. 23), in about four rows (Fig. 32)....*Sarcophaga* "E"
   Spines on anterior margin of Segment 2 mostly hair- or bristlelike; spines on Segment 2 inconspicuous (Fig. 34)....*Acridiophaga caridei**

9. Anterior margin of Segment 2 with three to five rows of pricklelike (Fig. 23) spines; first segment with many hairs on pleural area; oral hooks slender; distance from tip to anterodorsal angle of hypostomal sclerite equal to, or greater than, from hypostomal tip to nearest point in the pharyngeal sinus (Fig. 33)....*Sarcophaga* "D"
   Anterior margin of Segment 2 with but few prickle- or thornlike spines, most being bristlelike; first segment with only small group of bristles on the pleural areas; oral hooks stout, distance from tip of oral hook to anterodorsal tip of hypostomal sclerite about three-quarters that from tip of hypostomal sclerite to nearest point in sinus (Fig. 35)....*Acridiophaga aculeata*

10. Spines on mid venter between Segments 3 and 4 shorter than those between Segments 4 and 5; spines present on dorsum of Segments 1 to 4....11
    Spines between Segments 3 and 4 about equal to those between 4 and 5; spines present on dorsum of more than four anterior segments....13

11. Oral hooks sicklelike, lower profile of hook intersecting line from tip of hook to posterodorsal angle at center (Fig. 36)....*Blaesoxiphotheca coloradensis*
    Oral hooks not sicklelike, lower profile of hook intersecting line from tip of hook to posterodorsal angle at a point much nearer the tip....12

12. Long spines of pleural patches not divided at tips; spines in ventral bands between Segments 4 to 11 stout, seldom longer than twice basal width (Fig. 9)..*Blaesoxiphotheca* "A"
    Long spines of pleural patches frequently divided at tips; spines in ventral bands between Segments 4 to 11 less stout, longest usually more than twice basal width....*Blaesoxiphotheca* "B"

13. Greatest depth of oral hook about one-third distance from tip to anteroventral angle of basal area; spines in ventral bands between Segments 4 to 11 for the most part irregularly and openly spaced....*Blaesoxiphotheca* "C"
    Greatest depth of oral hook about one-half distance from tip to anteroventral angle of basal area; spines in ventral bands between Segments 4 to 11 mostly compact and evenly spaced (Fig. 10)....*Blaesoxiphotheca caudata*

14. Anterodorsal processes of pharyngeal plates well developed to form a continuous band or arch between the lateral plates (Fig. C)....*Kellymyia kellyi*
    Anterodorsal processes not developed to form connecting band....15

15. Only first segment with encircling spines (Fig. 16)....*Opsophyto opifera*
    Four or more segments with encircling spines....16

16. Seven or more segments with encircling spines....17
    Only first four segments with encircling spines; posterior margin of Segment 10 with long dorsolateral patches; a few coarse spines present dorsally (Fig. 11)..*Tephromyiella* "A"

17. Ventral fusiform areas about five rows of spines wide; spines short and conelike, scattered (Fig. 19)....*Tephromyiella atlanis*
    Ventral fusiform areas about 10 rows wide; spines in groups of two's and four's, in general appearance hirsute (Fig. 20)....*Tephromyiella neuquenensis*†

18. Heavily pigmented platelike spots on mid-dorsal surface of Segment 10; papillae on pleural areas of Segments 9 and 10 often with black basal ring (Fig. 21)....*Protodexia hunteri*
    No heavily pigmented platelike spots on mid-dorsal surface of Segment 10, but a group of four or five coarse spines on either side of mid-dorsal area; papillae on Segments 9 and 10 without black basal ring (Fig. 22)....*Protodexia australis*‡

* *South American species released in small numbers at Chatterton and Brighton, Ont.*

† *South American species released at Chatterton, Ont., and Carmangay, Alta.*

‡ *South American species released at Chatterton, Ont., at Carmangay, Alta., and in the Lac du Bois ranges of British Columbia.*

Sarcophaga reversa Ald.

Sarcophaga "A" Knipling, 1936, J. Parasitology, 22(5) : 444, Figs. 20, 45.

First-stage larva (Fig. 1) translucent white in color, tapering at anterior end, more rounded posteriorly; approximately 2.0 mm. in length and 0.5 mm. in diameter. Segments, except second, with dark spines ventrally; Segment 1 with several rows of coarse, pricklelike spines; those on Segment 2 much smaller and less conspicuous than those on adjoining segments. Spines on Segments 3 and 4 reduced on mid-dorsal line; Segment 5 with patch of dark spines on dorsolateral regions; spines reduced dorsally, leaving a mid-dorsal section without spines in length equal to four to eight times that of the longest spines in the lateral patch. Band on Segments 5 to 11 divided transversely on venter, the hinder section narrower and with smaller spines; bands of spines somewhat broader in pleural regions. Segments 3 to 10 have a scattering of hairs or bristles on the pleural areas.

The buccopharyngeal armature (Fig. 28) 0.3 mm. in length, with a pair of strong oral hooks that curve downward and outward, terminating in sharp tips; the anterior margin of basal area two-lobed in profile. Infrahypostomal bridge fused with the hypostomal sclerite.

The posterior cavity with a pair of two-lobed, sharp-tipped spiracles, the outer lobes longest. Below the spiracles, at the margins of the cavity, are a pair of clawlike processes with several sharp spines at the tip. Several short spines surround the anal opening. On the ventral surface of the posterior segment are two pairs of protuberances or swellings, the upper pair about twice as long as wide and somewhat pendulous, the lower pair larger and more rounded.

The usual antenno-maxillary complex is present on the pseudocephalon. Each thoracic segment bears a cluster of three divergent spines on the latero-ventral areas and two papillae on the pleural areas; each abdominal segment except the last bears a single papilla on each pleural area and the last has several in the region of the posterior cavity.

Sarcophaga "H"

First-stage larva (Fig. 2) translucent white in color, cylindrical, tapering toward anterior end, more rounded posteriorly; approximately 1.6 mm. in length and 0.4 mm. in diameter. Segments, except second, with dense dark band of spines ventrally; Segment 2 with fewer, lighter spines. Segment 1 with four to five rows of coarse spines, the smaller ones pricklelike, those on pleural and dorsal regions longer. Segment 2 with four to five rows of short, broad-based spines ventrally, a few longer ones in pleural regions, and only a scattering of small spines across the dorsum. Segments 3, 4, and 5 with each anterior margin encircled with band of spines; spines more dense ventrally and bands widest in the mid-pleural regions; Segment 3 with smallest spines over dorsum. Segment 5 with a small spineless area in the pleural regions between dorsal and ventral spines and occasionally a short mid-dorsal section

without spines, but this never longer than longest spine of dorsolateral group. Segments 6 to 11 with ventral band only. Segments 5 to 11 with ventral band transversely divided into broad anterior and narrow posterior portions; spines of anterior portion much longer. Segments 1 to 10 with scattering of hairs or bristles in the pleural areas, not continuing around venter.

The buccopharyngeal armature (Fig. 30) 0.26 mm. in length, with a pair of strong, fairly slender oral hooks curving downward and slightly outward at tips; distance from tip of hook to anterodorsal angle of hypostomal sclerite twice distance from tip to anterior margin of basal area. Infrahypostomal bridge fused with hypostomal sclerite.

Posterior cavity with a pair of two-lobed, sharp-tipped spiracles, a pair of clawlike processes with about five coarse spines at apex, and lightly pigmented spines on its floor. Extremely fine hairs also present on posterior surface of last abdominal segment. A number of coarse spines surround the anal opening. Four well developed lobes present near the opening; the upper two longer and bulbous, the lower pair much larger and more tumid.

The antenno-maxillary complex is well defined on the pseudocephalon; each thoracic segment bears a three-bristled organ on each ventrolateral area, and each thoracic and abdominal segment bears one or more sensory papillae.

Sarcophaga "C"

First-stage larva (Fig. 3) translucent white in color, cylindrical, tapering towards anterior end, more rounded posteriorly; approximately 1.5 mm. in length and 0.4 mm. in diameter. First six segments encircled with spines on each anterior margin; spines on first segment heavily pigmented, prickle-like with broad bases. Segment 2 with similar but smaller, less pricklelike spines except in pleural regions, where longer spines are present. Segments 3 to 6 encircled with dark, closely packed thornlike spines, much longer in pleural regions. Occasionally a few scattered spines on dorsolateral regions of Segment 7; Segments 7 to 11 each with dense band of spines on ventral anterior margin (or intersegmentally). Transverse spineless area occurs in ventral bands beginning at Segment 4 or 5, and continuous to Segment 11. A scattering of fine bristles is present on Segments 1 to 10, with most abundant and longest bristles in pleural regions, practically absent ventrally.

The buccopharyngeal armature (Fig. 31) 0.3 mm. in length, with the slender hooks of the mandibular sclerites curved gently downward and outward at the tips; hooks about one and one-half times as long as the basal area. The infrahypostomal bridge fused with the hypostomal sclerite.

The posterior cavity contains a pair of two-lobed, sharp-tipped spiracles with outer lobes longest, a patch of small spines on the floor of the cavity, and a clawlike process in each lateral margin with coarse spines at tip. Four to six coarse spines surround the anal opening; near the opening are four lobelike swellings, the lower pair large and rounded, the upper more bulbous with sensory papilla at each tip.

The usual antenno-maxillary complex present on the pseudocephalon and tribristled sensoria on the lateroventral areas of the three thoracic segments. Other sensory papillae are present on each thoracic and abdominal segment.

Sarcophaga "D"

First-stage larva (Fig. 5) translucent white in color, cylindrical, tapering at anterior end, more rounded posteriorly; approximately 1.5 mm. in length and 0.4 mm. in diameter. Segments, except second, with dense band of spines on anteroventral margins and Segments 1 to 9 with spines over dorsum. Segment 1 with four to five rows of coarse spines, some pricklelike with broad bases; Segment 2 with several rows of much smaller, less conspicuous spines; spines more scattered and in fewer rows dorsally. Segments 3 and 4 each encircled with dense band of well pigmented thornlike spines, somewhat longer in pleural regions. Segments 5 to 9 each with spines on anterior dorsolateral margin almost as dense as on ventral half; dorsolateral portion of band separated from ventral by short spineless section in pleural regions; spines on dorsal area of Segment 9 less dense than others; usually a spineless section on mid-dorsal line. Each of Segments 5 to 11 with ventral band transversely divided into broader anterior and narrower posterior portions, spines on anterior portion much longer. Segments 1 to 10 with plentiful scattering of fine bristles on pleural areas, less abundant on Segments 7 to 10.

The buccopharyngeal armature (Fig. 33) 0.3 mm. in length with a pair of strong, fairly slender oral hooks curving slightly downward and outward at tips. Length of hook greater than length of basal area of mandibular sclerite. Infrahypostomal bridge fused with hypostomal sclerite; pharyngeal wings as illustrated.

Posterior cavity with a pair of two-lobed, sharp-tipped spiracles, a pair of clawlike processes with spines at tips, and a patch of small, inconspicuous spines on its floor. Four small spines surround the anal opening and four lobes are present on the posteroventral surface of the last segment, the upper pair bulbous, the lower larger and more rounded.

The antenno-maxillary complex is well defined on the pseudocephalon and each thoracic segment bears a three-bristled organ on its ventrolateral surfaces. Small papillae are present on pleural areas of thoracic and abdominal segments.

Sarcophaga "E"

First-stage larva (Fig. 4) translucent white in color, cylindrical, tapering at ends; approximately 1.7 mm. in length and 0.5 mm. in diameter. The first seven segments each encircled with spines on the anterior margin, the remaining segments with heavy band of spines on the ventral surface. Segment 1 with five or six rows of dark pricklelike spines; Segment 2 with several rows of smaller pricklelike spines on anterior border, less conspicuous than those on adjoining segments. Spines on following segments more thornlike and much longer, especially on pleural areas; on Segments 6 and 7 the spines much reduced in size near the mid-dorsal line, and band on each of these two segments

frequently with a slight break in the pleural regions. Segments 4 to 11 each with ventral band divided into broad anterior and narrow posterior portions, the anterior portion with much longer spines, especially in the pleural regions. The pleural areas of Segments 1 to 10 also with bristly hairs, these continuing on to the ventral area of the segments.

The buccopharyngeal armature (Fig. 32) 0.3 mm. in length, with a pair of slender oral hooks about one and one-half times as long as the basal area; the hooks curving downward and outward toward the tips. The infrahypostomal bridge is fused with the hypostomal sclerite; profile of pharyngeal portion as illustrated.

The posterior cavity with the usual two-lobed, sharp-tipped spiracles, claw-like processes with spines at tips, and a patch of fine spines on its floor; very fine hairs occasionally apparent on rim of posterior cavity. Anal opening surrounded by 8 to 10 short spines. Four swollen lobes present on the postero-ventral region of the last abdominal segment; the lower pair large and rounded, the upper more bulbous, somewhat stalked, with a single papilla at each tip.

Sensory papillae, antenno-maxillary complex, and three-bristled sensoria as in *Sarcophaga* "C".

Acridiophaga caridei (Brèthes)

Acridiophaga caridei (Brèthes). de Crouzel, 1944, Proc. Entomol. Soc. Wash. 46(9) : 239-246. 2 Pl. 12 Fig.

First-stage larva (Fig. 6) translucent white in color, cylindrical, tapering at anterior end, more rounded posteriorly; approximately 1.3 mm. in length and 0.3 mm. in diameter. The first seven segments each encircled with spines on anterior margin; seventh with a considerable portion of mid-dorsal area without spines; occasionally Segment 8 with small dorsolateral patch. Segment 1 with wide band of six to seven rows of coarse spines, smaller and more pricklelike ventrally. Segment 2 with much less conspicuous row of almost bristlelike spines on anterior margin, spines somewhat stronger on ventral half of segment. Several rows of dense thornlike spines encircle Segments 3 and 4, with longest spines on pleural areas, becoming progressively smaller toward mid-dorsal line. Fairly dense band of thornlike spines present on ventral half of each Segment from 4 to 11, these bands divided transversely on venter with the anterior portion wider than the posterior, and longest spines on pleural ends of bands. Dorsolateral portions of encircling spines on each of Segments 5 to 7 slightly separated from spines on ventral half; spines less dense on the dorsal portion of segments. On the discal portion of the pleural areas of Segments 1 to 11 a scattering of fine bristles or hairs present and continuing on to the ventral surface of Segments 5 to 10 as a narrow band at the posterior margin of each segment.

The buccopharyngeal armature (Fig. 34) 0.23 mm. in length, with two fairly stout oral hooks curved downward and outward to sharp tips; the basal area is large. Distance from tip of hypostomal sclerite to anterior margin of basal area is three-fifths that from tip of hypostomal sclerite to tip of oral

hook. Distance from tip of oral hook to anterodorsal tip of hypostomal sclerite about equal to that from tip of hypostomal sclerite to nearest point in sinus; profile of wings as illustrated.

The posterior cavity with a pair of two-lobed, sharp-tipped spiracles, the outer lobes longer, a pair of clawlike processes with apical spines, and a small patch of spines on its floor. Several short spines surround the anal opening. Posteroventral surface of the last abdominal segment with four lobes, the upper pair smaller and somewhat pendulous, the lower ones larger and more rounded. Sensoria consist of the usual antenno-maxillary complex, three-bristled organs on the thoracic segments, and papillae on the thoracic and abdominal segments.

Acridiophaga aculeata (Ald.)

First-stage larva (Fig. 7) translucent white in color, cylindrical, tapering at anterior end, rounded posteriorly; approximately 1.5 mm. in length and 0.3 mm. in diameter. The first eight segments encircled with spines, and a small dorsolateral patch of spines usually present on Segment 9. Anterior margin of Segment 1 with five to eight rows of broad-based spines, these shorter and more pricklelike on the ventral surface. The spines on the anterior margin of Segment 2 usually scattered and inconspicuous, the spines only slightly broader at their bases than bristles. Segments 3 and 4 with band of dense thornlike spines on each anterior margin, spines much reduced in size near mid-dorsal line. Each of Segments 5 to 11 with band on ventral half divided transversely, with wider anterior portion of longer spines and bands slightly widened at upper ends. Dorsal portion of band on each of Segments 5 to 8 separated from ventral portion by slight gap; mid-dorsal break in bands slightly wider on Segments 7 and 8 than on anterior ones, and dorsolateral patch on Segment 9 reduced to a few spines. Segments 10 and 11 without dorsal spines. Hairlike bristles present on Segments 2 to 11 on discal areas below the mid-lateral line and continuing around venter on posterior regions of Segments 7 and 8.

The buccopharyngeal armature (Fig. 35) 0.23 mm. in length with two stout oral hooks curved slightly downward and outward at tips; basal area large, with anterior margin about two-thirds of distance from anterodorsal tip of the hypostomal sclerite to tip of the oral hook. Distance from dorsal tip of the hypostomal sclerite to tip of oral hook about two-thirds that from tip of hypostomal sclerite to nearest point in pharyngeal sinus. Infrahypostomal bridge fused with hypostomal sclerite; dorsal and ventral wings as illustrated.

The posterior cavity with the usual pair of two-lobed, sharp-tipped spiracles, a pair of clawlike processes with apical spines, and a scattering of small spines on the floor. The anal opening surrounded by about six short spines, and four fleshy lobes present on the posterior ventral surface of the last abdominal segment.

The pseudocephalon bears the antenno-maxillary complex and the thoracic segments the three-bristled sensoria; papillae are present on the thoracic and abdominal segments as described for *Sarcophaga reversa*.

Blaesoxiphotheca coloradensis (Ald.)

First-stage larva (Fig. 8) ivory white in color, cylindrical, tapering slightly toward both ends; approximately 1.6 mm. in length and 0.45 mm. in diameter. Clump of long spines, several rows in width (Fig. 40), present on posterior lateral areas of each of Segments 4 to 10, the lower spines in the groups progressively shorter from Segment 4 to 10; longest spines in anterior clump equal in length to that of oral hooks. The first four segments each completely encircled with spines on anterior margin. Spines on the first segment somewhat triangular in shape, 0.01 mm. in length, those in lateral regions with prickle-like tips. Spines on each anterior margin of Segments 2 to 4 five to nine rows wide, with the spines mostly small and inconspicuous. Forty or more well pigmented spines present on the posteroventral margin of each of Segments 4 to 10, these spines closely placed and sometimes apparently fused basally; in length about twice their basal width, some slightly hooked forward at their tips. A few rows of inconspicuous spines present on the anteroventral margin of Segments 5 to 8. Dorsally, Segments 5 to 11 free of spines.

The buccopharyngeal armature (Fig. 36) 0.34 mm. in length, with two crescent- or sickle-shaped oral hooks, these curved down and outward toward the tips. Lower profile of oral hook intersects line from tip of hook to posterodorsal angle of basal area at center. The infrahypostomal bridge articulated with hypostomal sclerite. Distance from anterior tip of hypostomal sclerite to nearest point in sinus about equal in length to that of the mandibular sclerite. Dorsal wing slim and well arched, slightly exceeding the broader ventral wing in length.

The posterior cavity with a pair of two-lobed, sharp-tipped spiracles; the outer lobes about twice as long as the inner ones. The cavity with a patch of 15 or 20 fine spines on the floor and laterally a pair of clawlike processes with about five coarse spines at their tips. Several spines surround the anal opening.

The antennae with a diameter about equal to their length. The thoracic segments with two papillae on each pleural area and each abdominal segment except the last with one papilla laterally. The ventrolateral surface of each thoracic segment with a three-bristled organ.

Blaesoxiphotheca "A"

First-stage larva (Fig. 9) ivory white in color, cylindrical, tapering slightly toward the ends; approximately 1.7 mm. in length and 0.4 mm. in diameter. It differs from *B. coloradensis* only in the form of the mouth parts (Fig. 37). The oral hooks less sickle-shaped, and the pharyngeal sinus not so deep as in *B. coloradensis*. Lower profile of oral hook intersects line from tip of hook to posterodorsal angle of basal area about one-quarter of the distance from tip. Distance from tip of hypostomal sclerite to nearest point of sinus over twice depth of sinus between dorsal and ventral wings.

Blaesoxiphotheca "B"

First-stage larva ivory white in color, cylindrical, tapering slightly towards ends; approximately 2.1 mm. in length and 0.65 mm. in diameter. Clumps of long spines present on Segments 4 to 10, these spines of irregular length and frequently divided at tips. The anterior margin of the first four segments completely encircled with spines; those on Segment 1 triangular in shape, those on Segments 2 and 3 similar but small and inconspicuous. Spines on Segment 4 somewhat larger on ventral half and many bifid at tips. Dorsal spines small and inconspicuous on Segments 2, 3, and 4, absent on Segments 5 to 11.

The buccopharyngeal armature similar to *Blaesoxiphotheca* "A". Lower profile of oral hook intersects line from tip of hook to posterodorsal angle of basal part at point about one-quarter of the distance from tip. Distance from tip of hypostomal sclerite to nearest point of sinus over twice depth of sinus from dorsal to ventral wing.

Blaesoxiphotheca "C"

First-stage larva similar to *B. caudata* but with anterodorsal spines to Segment 6 only. Spines in heavy ventral bands irregularly and more openly spaced, with length of longest spines about four times basal width.

Buccopharyngeal armature with lower profile of oral hook largely below line from tip of hook to posterodorsal angle of basal area. Distance from tip of hypostomal sclerite to nearest point of sinus three times depth of sinus. Greatest depth of oral hook equal to about one-third of the distance from its tip to anteroventral angle of basal area.

Posterior cavity with processes and spiracles as in *B. caudata*; sensoria also similar to those of *B. caudata*.

Blaesoxiphotheca caudata Tns.

First-stage larva (Fig. 10) ivory white in color, cylindrical, tapering slightly toward ends; approximately 1.3 mm. in length and 0.3 mm. in diameter. Patch of long spines (Fig. 39) present on pleura of Segments 4 to 10, these only two or three rows of spines in width and the spines uneven in length. Each of Segments 1 to 4 encircled with conspicuous band of spines, with largest spines in anterior rows; spines present on anteroventral margin of each of Segments 5 to 11, and dorsally on 5 to 9. Heavy spines on venter between Segments 3 and 4 about as large as those between 4 and 5; two to three times as many spines in band between Segments 4 and 5 as between Segments 10 and 11; spines evenly spaced and compact.

Buccopharyngeal armature (Fig. 38) 0.27 mm. in length, with a pair of stout, beak-shaped oral hooks; lower margin of hook falling below line from tip of hook to posterodorsal angle of basal area. Greatest depth of oral hook equal to about one-half of the distance from its tip to anteroventral angle of basal area. Infrahypostomal bridge articulated with hypostomal sclerite.

Distance from tip of hypostomal sclerite to nearest point of sinus two and one-half times depth of sinus from dorsal to ventral wing. The narrow dorsal wing curving gently backward and about one-third longer than the stouter ventral wing.

The posterior cavity with a pair of two-lobed, sharp-tipped spiracles, the outer lobes about twice as long as the inner. The cavity with 20 or more fine spines on its floor and at each lateral margin a clawlike process with four or five coarse spines at the tip. Four coarse spines and four swellings or lobes present near the anal opening.

Pseudocephalon with the usual antenno-maxillary complex, the antennae thimble-shaped and about 0.01 mm. long. Three-bristled sensoria present on the lateroventral surfaces of each thoracic segment. Small, inconspicuous papillae present laterally, on each segment except last, where several are present on rim of cavity.

Tephromyiella "A"

First-stage larva (Fig. 11) translucent white in color, cylindrical, tapering at ends; approximately 1.0 mm. in length and 0.2 mm. in diameter. Segments 1 to 4 completely encircled with spines, the first segment with a wide band of pricklelike spines five rows wide ventrally, reduced to two dorsally; ventral spines smallest, those in laterodorsal region largest. Segment 2 with smaller, broad-based spines, somewhat pricklelike, with largest spines in the anterior row and several additional rows of smaller spines on the venter. Third and fourth segments with one to two rows of closely placed triangular spines on each anterior margin, followed on venter with three discontinuous rows of smaller spines. Band of spines on venter of Segments 5 to 11 with a group of two to four large, coarse spines laterally. Anteroventral area on Segments 5 to 10 each with fusiform band of spines consisting of a conspicuous anterior row, a central scattering of fine spines, and a posterior row of somewhat heavier spines. A few anteriorly directed spines occur occasionally on each posteroventral margin of Segments 5 to 10. A small pleural patch of four to six spines present posteriorly on each of Segments 4 to 6. A patch of coarse spines present on the anterior dorsolateral regions of Segments 5 to 10, with the number of spines reduced progressively to Segment 10; median dorsal region of each of Segments 5 to 11 free of spines. A short row of anteriorly directed spines occurs on the posterior margin of Segment 10 in dorsolateral region. The large spines on the anterior dorsolateral regions of Segments 5 to 10, and at the ends of the ventral fusiform areas of Segments 5 to 10 serve to separate this species from *T. atlanis*.

The buccopharyngeal armature (Fig. 43) 0.23 mm. in length, with forwardly directed oral hooks. Length of mandibular sclerite about equal to distance from tip of hypostomal sclerite to nearest point in sinus. Infrahypostomal bridge articulated with hypostomal sclerite.

The posterior cavity contains a pair of two-lobed, sharp-tipped spiracles, and a pair of clawlike processes with four to five spines at their tips. Fine spines

on the floor of the cavity can be seen only with difficulty. A few spines present in the region of the anal opening.

The antenno-maxillary complex present on the pseudocephalon and sensory papillae present on the thoracic and abdominal walls. Three-bristled organs not apparent on the thoracic segments.

Tephromyiella atlanis (*Ald.*)

First-stage larva (Fig. 13) translucent white in color, cylindrical, tapering toward anterior end, more rounded on posterior end; approximately 1.2 mm. in length and 0.25 mm. in diameter. Segments 1 to 7 each almost completely encircled on anterior margin with backwardly directed spines. Segments 9 and 10 encircled with anteriorly directed spines on their posterior margins. The bands of spines on Segments 5 to 7 interrupted in pleural regions, and with a patch of spines between dorsal and ventral bands. Segments 8 and 9 without band of spines but occasionally with a few isolated spines on anterodorsal margins. Spines on first segment pricklelike with broad bases, band five rows wide ventrally, reduced to two dorsally. Spines on anterior margin of Segment 2 also somewhat pricklelike but smaller. Spines on Segments 3 and 4 stout, well pigmented, closely placed, conelike in shape, and in bands one to two rows wide with a few smaller spines behind. Segments 6 to 10 with a single row of anteriorly directed spines on posteroventral margin. Fusiform band of spines on venter of each of Segments 5 to 10, five to six rows wide with largest spines in anterior row, spines short and conelike, those in center of each area well spaced and discrete (Fig. 19). Spines on anteroventral margin of Segment 11 similar to those on Segment 10 but without fusiform area.

Buccopharyngeal armature (Fig. 45) 0.22 mm. in length with oral hooks tapering toward tip. Ventral profile of hook relatively straight but depressed slightly on apical third; basal area of mandibular sclerite rectangular in outline and about twice as long as wide. Infrahypostomal bridge not fused but articulated with hypostomal sclerite; mandibular sclerite in length about three-quarters of the distance from tip of hypostomal sclerite to nearest point of sinus.

Posterior cavity with a pair of two-lobed, sharp-tipped spiracles and a pair of clawlike processes with apical spines; spines not apparent on floor of cavity. A few spines present in region of anal opening.

The antenno-maxillary complex present on the pseudocephalon and the usual papillae present on the thoracic and abdominal segments; the three-bristled sensoria not apparent on the thoracic segments.

Tephromyiella neuquenensis Bl.

First-stage larva (Fig. 12) ivory white in color, cylindrical, tapering toward anterior and posterior ends; approximately 1.1 mm. in length and 0.2 mm. in diameter. Rows of spines encircle Segments 1 to 8, 10, and 11. Spines on the first anterior segment in five irregular rows relatively large (up to 0.01 mm.) and pricklelike. Band of spines on Segment 2 less conspicuous than

those on adjoining segments; spines in about five rows, small except for a few larger ones in mid-pleural regions. Spines on the anterior margin of Segment 3 in three to five rows, the anterior row with larger spines in pleural regions. Spines on ventral surface of Segments 4 to 11 more thornlike. The small dorsal spines less abundant from Segment 3 to 7, absent on Segments 8 and 9, but present on Segments 10 and 11. The fusiform patches of spines on the ventral surface with somewhat hirsute appearance (Fig. 20), spines finer than the shorter, more conelike ones of *T. atlanis*. Spines at widest part of bands 8 to 10 rows in width and occurring in groups of two's and three's rather than singly as in *T. atlanis*.

The buccopharyngeal armature (Fig. 44) about 0.24 mm. in length, similar to that of *T. atlanis* and differing in no essential respects. In some specimens the oral hooks less stout than in *T. atlanis* but this feature somewhat variable.

The posterior cavity, spiracles, spines, and clawlike processes not distinguishable from those of *T. atlanis*.

Opsophyto opifera (Coq.)

First-stage larva (Fig. 16) translucent to ivory white in color, cylindrical, anterior end tapered, posterior end more rounded; approximately 1.3 mm. in length and 0.5 mm. in diameter. Body without spines except on the anterior margin of the first thoracic segment, which has two to three rows of small, backwardly directed, sharp, pricklelike spines, the spines small in dorsal area and larger in ventral region.

The buccopharyngeal armature (Fig. 41) 0.17 mm. in length, with two fine, sharp oral hooks. These about equal in length to that of the basal area, with axis of oral hook making approximately a 45° angle with axis of basal area; apical half of hook curved gently downward. Infrahypostomal bridge articulated with hypostomal sclerite. The distance from tip of hypostomal sclerite to nearest point in the sinus about three times depth of sinus from dorsal to ventral wing. The dorsal wing curves strongly upward then backward to narrow, tapered tip; the ventral wing broad.

The posterior cavity shallow, bearing a pair of two-lobed, sharp-tipped spiracles, the outer lobes about twice as long as the inner. Below spiracles a pair of clawlike processes with two or three apical spines; no spines apparent on floor of cavity but a few present about the anal opening.

The antenno-maxillary complex present on the pseudocephalon but sensory papillae not apparent on the thoracic or abdominal segments.

Protodexia hunteri (Hough)

First-stage larva (Fig. 14) translucent white in color, dorsoventrally flattened, and tapering toward the ends; approximately 1.0 mm. in length and 0.15 mm. in width. Spines inconspicuous except at higher magnifications, when fine intersegmental spines are evident. Several discontinuous rows of spines occur on the anterior margin of first segment, those on dorsal area

smaller. Second segment with four to five discontinuous rows of small spines on the anterior margin. Third and fourth segments with similar, somewhat narrower rows with some larger spines on each ventral half. Segments 5 to 10 devoid of spines on the pleural regions; Segments 5 to 8 with two to three rows of fine spines dorsally, terminating laterally in a few larger, scalelike spines. Ventral bands on same segments with six to seven rows of fine spines, with few larger spines at ends of bands. Dorsal spines on Segment 9 restricted to central portion and few in number (Fig. 21). Dorsal spines on Segment 10 heavily pigmented, scale- or platelike, and six to eight in number. These spines are a good specific character.

Buccopharyngeal armature (Fig. 46) 0.15 mm. in length, with scalpel- or leaflike oral hooks anteroventral angle of their basal areas extended downward and forward in profile. Infrahypostomal bridge articulated with hypostomal sclerite; form of dorsal and ventral wings as illustrated.

Posterior cavity (Fig. 21) with a pair of single-lobed, sharp-tipped spiracles. No clawlike processes present. Nine or more conspicuous spines on the floor, these usually in about two rows. A few coarse spines surround the anal opening.

Pseudocephalon with the usual antenno-maxillary complex. At higher magnification a single papilla distinguishable on pleural areas of abdominal segments; papillae about twice as long as wide and slightly curved, those on Segment 10 and occasionally on 9 with well pigmented ring around base. Stomatalike sensoria scattered over body surface.

Protodexia australis Bl.

First-stage larva (Fig. 15) translucent white in color, dorsoventrally flattened, and tapering toward the ends; approximately 1.0 mm. in length and 0.15 mm. in width. Spines present intersegmentally (or on anterior margins of segments) but inconspicuous except at higher magnifications. About four rows of pricklelike spines present on anterior margin of Segment 1, largest on ventral surface. Margin of Segment 2 encircled anteriorly with four to five discontinuous rows of fine spines. Third and fourth segments encircled with fine spines, the bands reduced almost to single row in lateroventral and laterodorsal regions. On the venter of each of Segments 3 to 7 band widened to five or eight rows with a few larger spines laterally. Band on dorsum of each of Segments 5 to 8 with about four and on dorsum of Segments 9 and 10 with one or two rows of fine spines and a few coarse spines at ends of bands. No heavily pigmented platelike spines on dorsal surface of Segment 10, only a row of fine spines with four or five coarse ones at the ends.

Buccopharyngeal armature (Fig. 47) 0.15 mm. in length, with scalpel- or leaflike oral hooks and anteroventral angle of basal area extended downward and forward. Infrahypostomal bridge articulated with hypostomal sclerite; wings as illustrated.

Posterior cavity with pair of single-lobed, sharp-tipped spiracles; no clawlike processes present; floor of cavity with 12 or more dark spines in several rows.

Pseudocephalon with antenno-maxillary complex, and abdominal segments with single papilla on each pleural area, those on Segments 9 and 10 lacking dark ring present on *P. hunteri*. Stomatalike pores or sensoria scattered over body.

Kellymyia kellyi (Ald.)

Sarcophaga kellyi Ald. Knipling, 1936, J. Parasitology, 22(5) : 442. Figs. 16, 42, 58, 75.

First-stage larva translucent white in color, cylindrical, tapering more toward anterior end; approximately 2.5 mm. in length and 0.7 mm. in diameter. Anterior margins of Segments 1 to 5 each with conspicuous band of spines. Band on Segment 1 almost twice as wide ventrally as dorsally. Spines on dorsal portion of Segment 5 less conspicuous than those on preceding segments; those on Segment 6 even less conspicuous. Broad ventral band on each of Segments 4 to 11 with transverse spineless area in center. A few rows of forwardly directed spines occur on the posteroventral margin of each of Segments 3 to 10; those on 9 and 10 more thornlike dorsally, completely encircling the segments; those on Segment 8 indistinct.

The buccopharyngeal armature (Fig. C) 0.25 mm. in length, with the usual pair of oral hooks and an articulated infrahypostomal bridge. Anterior dorsal processes of the pharyngeal plates united to form a joining arch or band.

The posterior cavity with a pair of large spiracles but no clawlike processes and no spines on its floor. The spiracles (Fig. F) two-lobed, oval in outline and associated with large felt chambers.

The antenno-maxillary complex well developed, the antennae 0.02 mm. in length and 0.007 mm. in diameter. Two-bristled sensoria present on the first two thoracic segments, three-bristled sensoria present on the third thoracic segment; very small papillae present on the thoracic and abdominal segments.

TACHINIDAE

Four species of tachinids have been reared from grasshoppers in the present study. These are *Euacemyia tibialis* (Coq.), *Ceracia dentata* (Coq.), *Hemithrixion oestriforme* B.B., and *Paradionaea atra* (Tns.). The last-named species has been taken from Ontario points only and only on a few occasions.

None of the tachinid species has been propagated in the laboratory and the following specific determinations have yet to be verified. However, first-stage larvae of *E. tibialis*, taken from gravid females and examined while still within the chorion, give reason to believe that the larvae of this species are correctly identified. Identity of the others has been deduced from the emergence of certain species of adults from the same or related collections of grasshoppers that contained larvae of a particular type.

According to Townsend (35, Pt. IV, p. 73) this group of flies, with the exception of *Paradionaea*, deposits its eggs upon the host and the larvae gain entry through the host integument.

The first- and second-stage larvae of these tachinids lie free within the coelomic cavity of the host, and the last two instars are provided with an integumental funnel. These funnels are most often attached in the thoracic region of the grasshopper.

The chief distinguishing characters used in the separation of the species are the shape of the infrabuccal plate and the kind and distribution of the spines in the second larval instar.

Key to Second-stage Tachinid Larvae*

1. Length of infrabuccal plate about equal to or less than greatest width 2
   Length of infrabuccal plate one and one-third times greatest width; teeth present on more than half marginal arc (Fig. 48) ..... *Hemithrixion oestriforme*
2. Spines present on anteroventral margin of second thoracic segment; spines on anteroventral margin of Segments 5 to 10 scalelike, apparent at lower magnifications (×50) ..... *Euacemyia tibialis*
   Spines absent on anteroventral margin of second thoracic segment; spines on other segments small, not scalelike 3
3. Greatest width of infrabuccal plate less than length; tips of arc directed toward base of stem ..... *Paradionaea atra*
   Greatest width of infrabuccal plate exceeding length; tips directed laterally .. *Ceracia dentata*

Hemithrixion oestriforme B.B.

Second-stage larva (Fig. 24) ivory white in color, cylindrical with rounded ends; approximately 1.0 mm. in length and 0.3 mm. in diameter. Band of spines present on the anteroventral margin of each of Segments 2 to 10; those on Segments 3 and 4 consisting of one or two rows of small, inconspicuous spines. Spines on Segment 2 pricklelike, in four or five rows, the rows slightly longer than the greatest width of infrabuccal plate. Segments 5 to 10 with larger, scalelike spines in two to three interrupted rows. Segment 5 with 12 to 14 small, conelike spines on lateral areas. Dorsal surface of segments with a scattering of very minute black dots.

The buccopharyngeal armature (Fig. 48) about 0.15 mm. in length, bearing a single median tooth with a finely serrated anterior margin; a dorsal accessory tooth apparent but not large. The lateral anterior plates, present on either side of the median hook each with the ventral tip curved backward. Infrabuccal sclerite or plate (Fig. 48) 0.08 mm. in length, the stem about equal in length to chord of marginal arc; central three-fifths of marginal arc with teeth.

Small two-lobed spiracles occur on the posterior surface of the last abdominal segment.

The antenno-maxillary complex present on the pseudocephalon; the antennae well pigmented and diameter twice the length.

* *These were originally believed to be first-stage larvae, but are now considered to be second-stage. Those found in eggs in gravid females and a few recently found in grasshoppers have lacked the infrabuccal plate and are considered to be first-stage.*

Euacemyia tibialis (Coq.)

Second-stage larva (Fig. 25) ivory white in color, cylindrical with rounded ends; approximately 1.8 mm. in length and 0.5 mm. in diameter. Band of spines present on the anteroventral margin of each of Segments 2 to 10, but inconspicuous on Segments 3 and 4. A short band of four to five rows present on Segment 2. Segments 5 to 10 with two to three rows of larger, scalelike spines, these spines about twice as wide (0.01 mm.) as long, with a single sharp tip at apex of each.

Pleural areas of Segment 5 with a small patch of 12 to 15 backwardly directed spines; occasionally a few present laterally on Segment 6. The dorsal surface of the larva with a scattering of very minute dots.

The buccopharyngeal armature (Fig. 49) approximately 0.2 mm. in length, bearing a single median tooth with the anterior margin finely serrated; the ventral tip of tooth acute and the posterior margin forming an obtuse angle with the lower margin of the anterior region; the upper margin of the tooth rounded into that of the anterior region. The dorsal wing large and heavily pigmented, its length three times its greatest width; the ventral wing very lightly pigmented, about two-thirds the length of the dorsal wing and slightly expanded on its apical two-fifths. The lateral anterior plates present on either side of the anterior region of the median hook, triangular to crescent-shaped with the ventral tip directed backward. Infrabuccal plate (Fig. 49) 0.08 mm. in length and about as long as chord of the marginal arc; the plate fan-shaped, with seven or more coarse teeth on the central half of its outer margin.

Small posterior spiracles present at tip of felt chambers on the posterior surface of the last abdominal segment (Fig. J).

The antenno-maxillary complex present on the pseudocephalon; the antennae half as long as wide and well pigmented.

Paradionaea atra (Tns.)

Second-stage larva (Fig. 27) ivory white in color, cylindrical with rounded ends; approximately 2.0 mm. in length and 0.65 mm. in diameter. Spines on ventral surface of Segments 3 to 10 apparent at higher magnifications (× 200) only; the spines in one or two rows and dotlike. No spines present on Segment 2.

Infrabuccal plate (Fig. 51) 0.85 mm. in length, with the lateral tips of the marginal arc directed toward base of stem, giving the plate an anchorlike form.

The single specimen with these characteristics is tentatively considered to be of this species, although the different form of the plate may be due to incomplete chitinization.

Ceracia dentata (Coq.)

Second-stage larva (Fig. 26) ivory white in color, cylindrical with rounded ends; approximately 2.5 mm. in length and 0.7 mm. in diameter. No spines apparent on the body except at higher magnifications, when two or three

rows of inconspicuous intersegmental spines are visible on the ventral surface. A patch of 10 to 12 very fine spines also present laterally on Segment 5.

The buccopharyngeal armature (Fig. 50) 0.28 mm. in length, with a single median tooth, its anterior margin finely serrated with downwardly directed teeth. Posterior edge of the median tooth curves into lower margin of the anterior region. The dorsal wing heavily pigmented, in length two and one-half times its greatest width. Ventral wing much narrower and more lightly pigmented, about two-thirds length of the dorsal wing and widened apically. Lateral anterior plates on either side of the median hook triangular in outline. Infrabuccal plate (Fig. 50) 0.1 mm. in length, somewhat T-shaped, with chord of arc greater than length of plate; tips of arc extended directly outwards. Central half of marginal arc with seven or more coarse teeth.

Posterior spiracles present on posterior surface of the last abdominal segment, these bilobed and appearing at tips of elongate felt chambers.

The usual antenno-maxillary complex present on the pseudocephalon, antennae well chitinized, with a diameter about twice the length.

Nemestrinidae

Two species of Nemestrinidae, *Parasymmictus clausus* O.S. and *Neorhynchocephalus sackenii* (Will.), are known to occur in British Columbia as parasites of grasshoppers (31) and it is probable that these two species are also present on the prairies. Unfortunately the larvae of these species are not sufficiently well known to permit recognition except to family. The immature stages of a species of *Neorhynchocephalus* which occurs in Argentina are well described and illustrated by de Crouzel and Salavin (8). Those of *Trichopsidea oestracea* West., a grasshopper parasite in Australia, have been described by Fuller (9).

The nonmuscoid type of mouth parts, the long breathing tube, and circular posterior spiracles are characteristic features of these larvae. From the paper on *Hirmoneura obscura* Meig. by Handlirsch (17) it would appear that the earliest-stage larvae recognized in the grasshoppers dissected in the present investigations are the second, although de Crouzel and Salavin's description (8) indicates that the transformation from first to second stage takes place within the host.

Observations by Spencer (29) make it apparent that parasitism of grasshoppers by nemestrinids is dependent largely on chance, since the eggs are laid in the vicinity of grasshoppers and not directly on them.

Anthomyiidae

Adults of the anthomyiid *Acridomyia canadensis* Snyder have been reared frequently from grasshoppers collected in the Prairie Provinces, and it is assumed that the immature stages of *Acridomyia* encountered in dissections are all of this species. One other species, *A. fumisquama* Snyder, described from North America (28) occurs in North Carolina and is considered to have a more southerly distribution.

Rukavishnikov (25) has given a rather complete description of some of the morphological features, particularly of the rasping mouth parts, of the adult of *A. sacharovi* Stakl. He has also given considerable information on the biology of this species and its value as a parasite of *Locusta migratoria* L. in the lower course of the Syr-Darja River in Kazakstan.

The mature and second-stage larvae are readily distinguished by the widely spaced and almost circular posterior spiracles. As previously mentioned, the genus *Acridomyia* includes the only species so far encountered that deposits its eggs within the body cavity of the grasshopper. It is probable that the large number of *Acridomyia* eggs and larvae frequently found in single hosts results from this method of attack.

Acridomyia canadensis Snyder

First-stage larva (Fig. 17) translucent to ivory white in color; approximately 0.6 mm. in length and 0.25 mm. in diameter, with body free of spines and the segmentation not readily discernible.

The buccopharyngeal armature (Fig. 42) simple, with a single median tooth; the narrow dorsal wing rising almost perpendicularly from the short ventral wing and curving gently backward.

The form of the posterior spiracles and of the antenno-maxillary complex have not been determined and it has not been possible to demonstrate their presence in the larval material prepared to date.

Note: *A. canadensis* may be present in its egg stage also, since this species deposits its eggs inside the body of the host. These are white in color, elongate-oval in shape, 0.5 mm. in length, and 0.2 mm. in diameter.

Acknowledgments

Many members of the western laboratories of the Division of Entomology, Dominion Department of Agriculture, have assisted in the collection of grasshoppers in the present co-operative project, but special credit is due H. W. Moore for his personal effort and interest in supervising the collecting and the sorting of the western grasshopper material on which the present information is largely based.

References

1. ALDRICH, J. M. Sarcophaga and allies in North America. Thomas Say Foundation. Lafayette, Indiana. 1916.
2. BEQUAERT, J. Notes on American Nemestrinidae, second paper. J. N.Y. Entomol. Soc. 42 : 163-184. 1934.
3. BEQUAERT, J. C. Catalogue of recent and fossil Nemestrinidae of America north of Mexico. Psyche, 54 : 194-207. 1947.
4. BUCKELL, E. R. and SPENCER, G. J. A preliminary list of the flesh flies of British Columbia. Proc. Entomol. Soc. Brit. Columbia, 42 : 6. 1945.
5. CURRAN, C. H. The nearctic species of the nemestrinid genus *Rhynchocephalus* Fischer, (Diptera). Can. Entomologist, 63 : 68-72. 1931.
6. CURRAN, C. H. Families and genera of North American Diptera. Ballou Press, New York. 1934.

7. DE CROUZEL, IRMA SANTORO. First instar larva of *Acridiophaga caridei* (Brèthes), (Diptera: Sarcophagidae). Proc. Entomol. Soc. Wash. 46 : 239-246. 1944.
8. DE CROUZEL, IRMA SANTORO and SALAVIN, RAIMUNDO G. Contribución al estudio de los *Neorhynchocephalus*. Argentinos (Diptera: Nemestrinidae). Anales soc. cient. argentina, 136 : 145-177. 1943.
9. FULLER, MARY E. Notes on *Trichopsidea oestracea* (Nemestrinidae) and *Cyrtomorpha flaviscutellaris* (Bombyliidae)—two dipterous enemies of grasshoppers. Proc. Linnean Soc. N.S. Wales, 63 : 95-104. 1938.
10. FULLER, MARY E. On the biology and early stages of *Helicobia australis* J. & T. (Sarcophagidae), a dipterous insect associated with grasshoppers. Proc. Linnean Soc. N.S. Wales, 63 : 133-138. 1938.
11. GRAHAM, K. Variations within the species of the nemestrinid fly *Rhyncocephalus sackeni* Will. Can. Entomologist, 64 : 167-168. 1932.
12. GREENE, C. T. Illustrated synopsis of the puparia of 100 muscoid flies (Diptera). Proc. U.S. Natl. Museum, 60 (art. 10) : 1-39. 1921.
13. GREENE, C. T. The puparia and larvae of sarcophagid flies. Proc. U.S. Natl. Museum, 66 (art. 29) : 1-26. 1925.
14. HALLOCK, HAROLD C. The Sarcophaginae and their relatives in New York, Part I. J. N.Y. Entomol. Soc. 48 : 127-153. 1940.
15. HALLOCK, HAROLD C. The Sarcophaginae and their relatives in New York. II. J. N.Y. Entomol. Soc. 48 : 201-231. 1940.
16. HALLOCK, HAROLD C. The Sarcophaginae and their relatives in New York. II. J. N.Y. Entomol. Soc. 50 : 215-241. 1942.
17. HANDLIRSCH, A. Die Metamorphose und Lebenweise von *Hirmoneura obscura* Meig., einem Vertreter der Dipteren-Familie Nemestrinidae. Wien. Entomol. Z. 2 : 11-15. 1883.
18. HAYES, WILLIAM P. and DECOURSEY, J. D. Observations of grasshopper parasitism, in 1937. J. Econ. Entomol. 31 : 519-522. 1938.
19. KEILIN, D. Recherches sur les larves de diptères cyclorhaphes. Bull. Sci. France Belg. 49 : 15-198. 1916.
20. KELLY, E. O. G. A new sarcophagid parasite of grasshoppers. J. Agr. Research, 11 : 435-443. 1914.
21. KNIPLING, EDWARD F. A comparative study of the first instar larvae of the genus *Sarcophaga* (Calliphoridae, Diptera) with notes on the biology. J. Parasitol. 22 : 417-454. 1936.
22. LAHILLE, F. La langosta y sus Moscas parasitarias. Anales Ministerio de Agr., Seccion de Zootecn., Bact. Vet. y Zool. 3 : 1-136. 1907.
23. OLSAUFIEV, N. G. [A study of flies parasitic on the Asiatic locust (*Locusta migratoria* L.) and their superparasites. Parasites of the larvae and full-grown insects.] Rept. Bur. Applied Entomol. (Leningrad), 4 : 61-120. 1929.
24. POTGIETER, J. T. A contribution to the biology of the brown swarm locust *Locusta pardalina* Wlk. and its natural enemies. Pan-African Agr. Vet. Conf. Pretoria. 265-308. 1929.
25. RUKAVISHNIKOV, B. I. [Contribution to the study of flies parasitic on the larval and adult instars of the migratory locust.] Plant Protection (U.S.S.R.), 1 : 191-261. 1930.
26. SMITH, R. W. Observations on parasites of some Canadian grasshoppers. Can. Entomol. 76 : 28-33. 1944.
27. SNODGRASS, R. E. Anatomy and metamorphosis of the apple maggot *Rhagoletis pomonella*. J. Agr. Research, 28 : 1-36. 1924.
28. SNYDER, FRED M. The genus *Acridomyia* Stackelberg in North America (Diptera: Muscidae). Am. Museum Novitates, No. 1076. 1940.
29. SPENCER, G. J. The oviposition habits of *Rhyncocephalus sackeni* Will. (Diptera: Nemestrinidae). Proc. Entomol. Soc. Brit. Columbia, 28 : 21-24. 1931.
30. SPENCER, G. J. Notes on *Rhyncocephalus sackeni* Will., a correction (Nemestrinidae: Diptera). Can. Entomol. 66 : 87. 1934.
31. SPENCER, G. J. Notes on the tanglewing flies of British Columbia. (Diptera: Nemestrinidae). Proc. Entomol. Soc. Brit. Columbia, 42 : 18. 1945.
32. THOMPSON, W. R. Recherches sur les diptères parasites. Bull. Biol. France Belg. 54 : 313-463. 1921.
33. THOMPSON, W. R. Les larves primaires des tachinaires à œufs microtypes. Ann. de parasitol. humaine et comparée, 2 : 185-201 and 279-306. 1924.

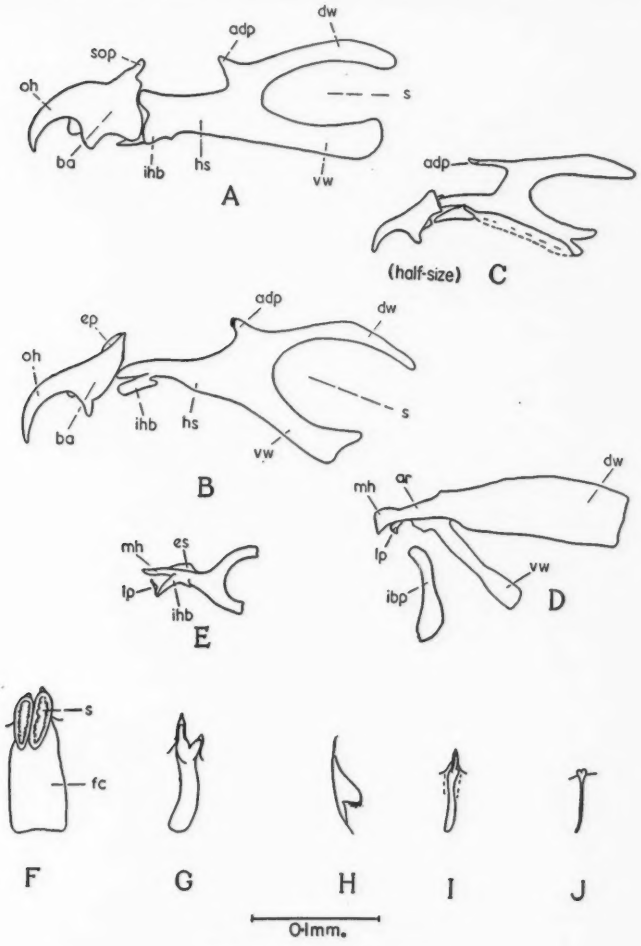
34. TONNOIR, A. L. On the taxonomy of *Helicobia australis* (Sarcophaginae) a dipterous insect associated with grasshoppers. Proc. Linnean Soc. N.S. Wales, 63 : 129-132. 1938.

35. TOWNSEND, C. H. T. Manual of myiology. 12 vol. Charles Townsend and Filhos, Itaquaquecetuba, Saõ Paulo, Brazil. 1934–1942.

36. UVAROV, B. P. Locusts and grasshoppers. A handbook for their study and control. Imp. Bur. Entomol. (London). 1928.

37. WOOD, A. H. Studies on some dipterous parasites of *Schistocerca* and *Locusta* in the Sudan. Bull. Entomol. Research, 24 : 521-530. 1933.

(Figs. A to J and 1 to 50 follow.)



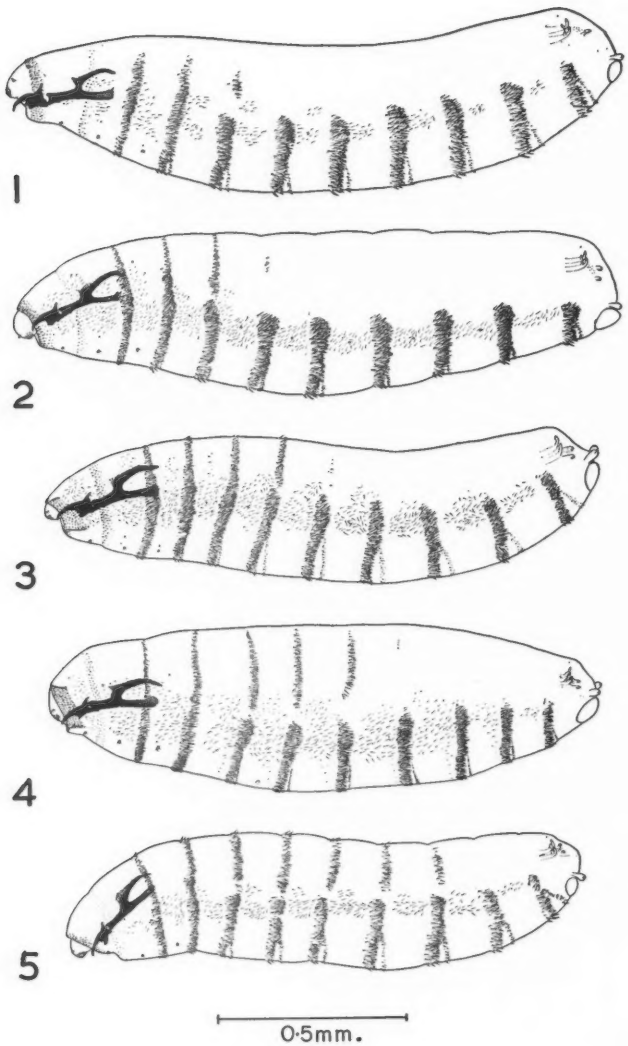
EXPLANATION OF FIGURES

FIGURES A TO E *are of the buccopharyngeal armatures of the species indicated.*

A. *Sarcophaga reversa* Ald.
B. *Blaesoxiphotheca coloradensis* (Ald.)
C. *Kellymyia kellyi* (Ald.)
D. *Euacemyia tibialis* (Coq.)
E. *Acridomyia canadensis* Snyder.

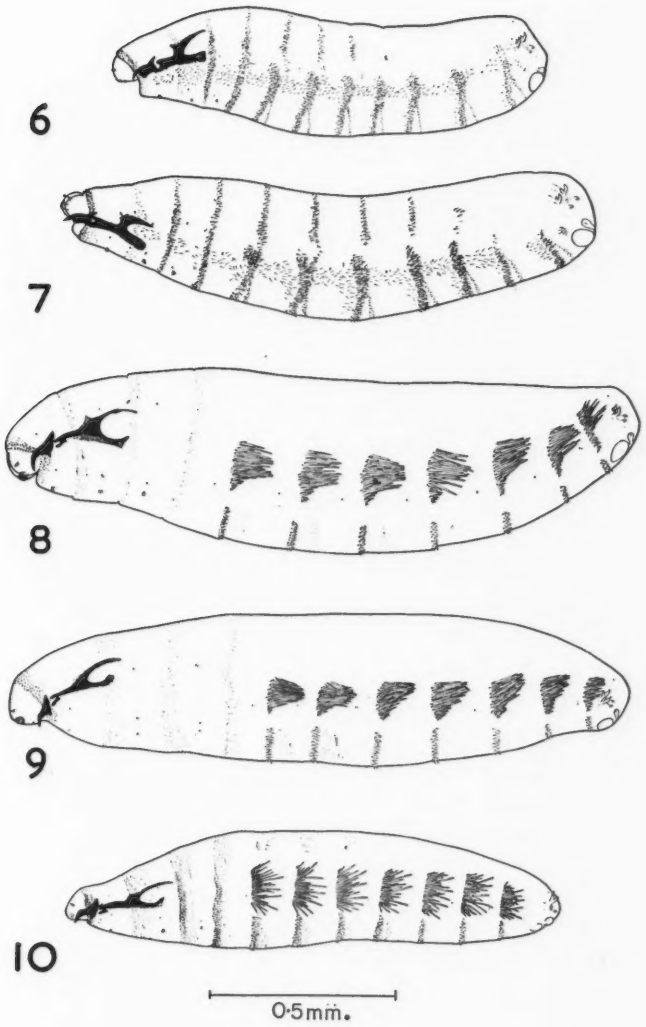
adp, anterior dorsal process; ar, anterior region; ba, basal area of mandibular sclerite; dw, dorsal wing; ep, es, epipharyngeal sclerite; hs, hypostomal sclerite; ibp, infrabuccal plate; ihb, infrahypostomal bridge; lp, lateral plate; mh, median hook; oh, oral hook; s, sinus; sop, supraoral process; vw, ventral wing.

F. *Posterior spiracle of K. kellyi. s, spiracular slit; fc, felt chamber.*
G. *Posterior spiracle and felt chamber of S. reversa.*
H. *Clawlike process of posterior cavity of S. reversa.*
I. *Posterior spiracle and felt chamber of P. hunteri.*
J. *Posterior spiracle and felt chamber of E. tibialis.*



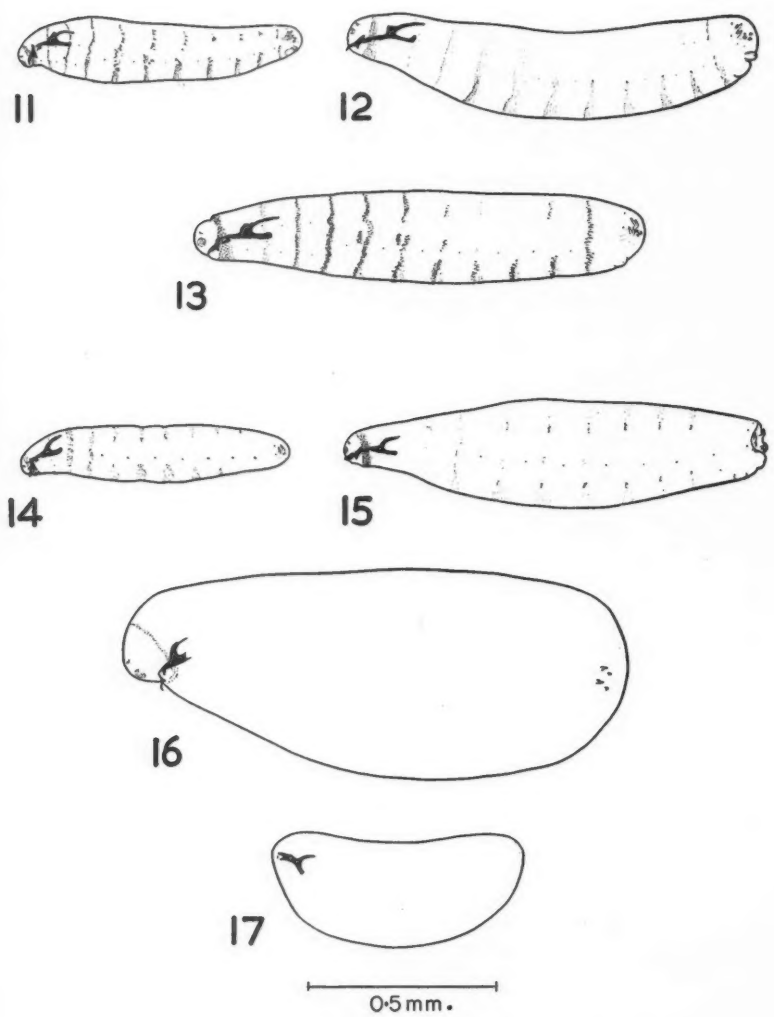
First-instar Larva

FIG. 1. *Sarcophaga reversa*. FIG. 2. *Sarcophaga* "H". FIG. 3. *Sarcophaga* "C" FIG. 4. *Sarcophaga* "E". FIG. 5. *Sarcophaga* "D".



First-instar Larva

FIG. 6. *Acridiophaga caridei.* FIG. 7. *Acridiophaga aculeata.* FIG. 8. *Blaesoxiphotheca coloradensis.* FIG. 9. *Blaesoxiphotheca* "A". FIG. 10. *Blaesoxiphotheca caudata.*



First-instar Larva

FIG. 11. *Tephromyiella* "A". FIG. 12. *Tephromyiella neuquenensis.* FIG. 13. *Tephromyiella atlanis.* FIG. 14. *Protodexia hunteri.* FIG. 15. *Protodexia australis.* FIG. 16. *Opsophyto opifera.* FIG. 17. *Acridomyia canadensis.*

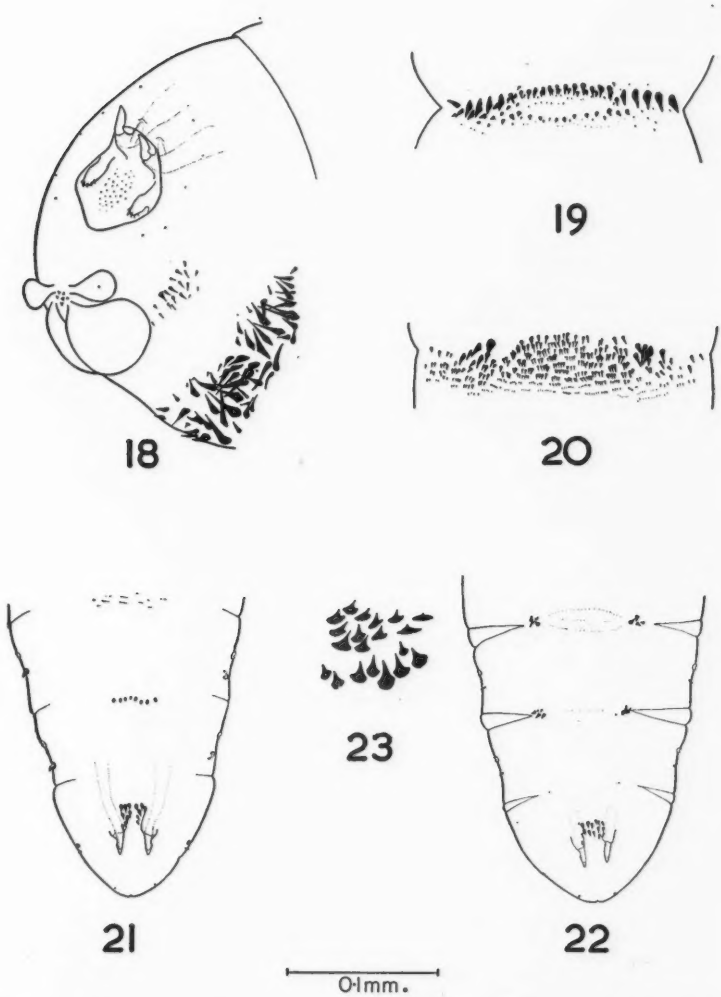
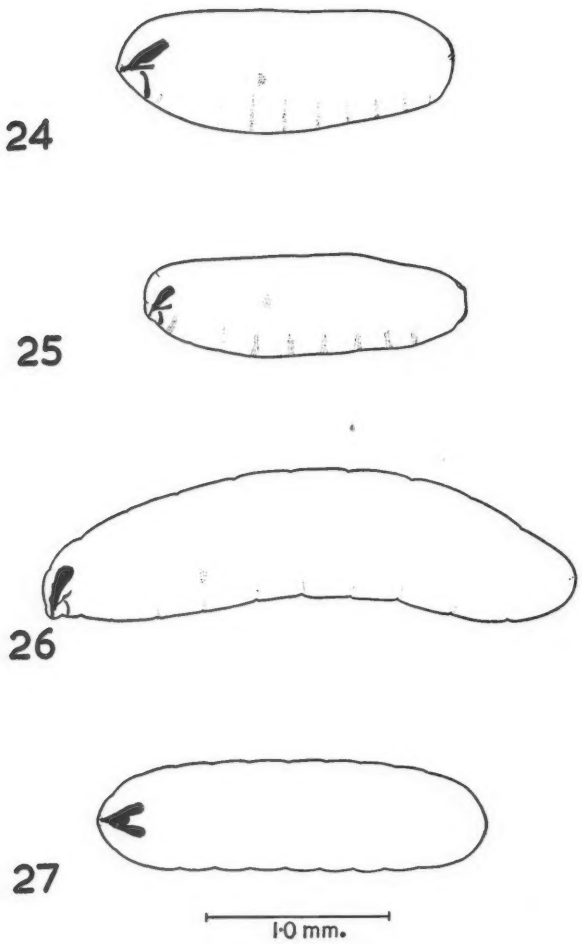
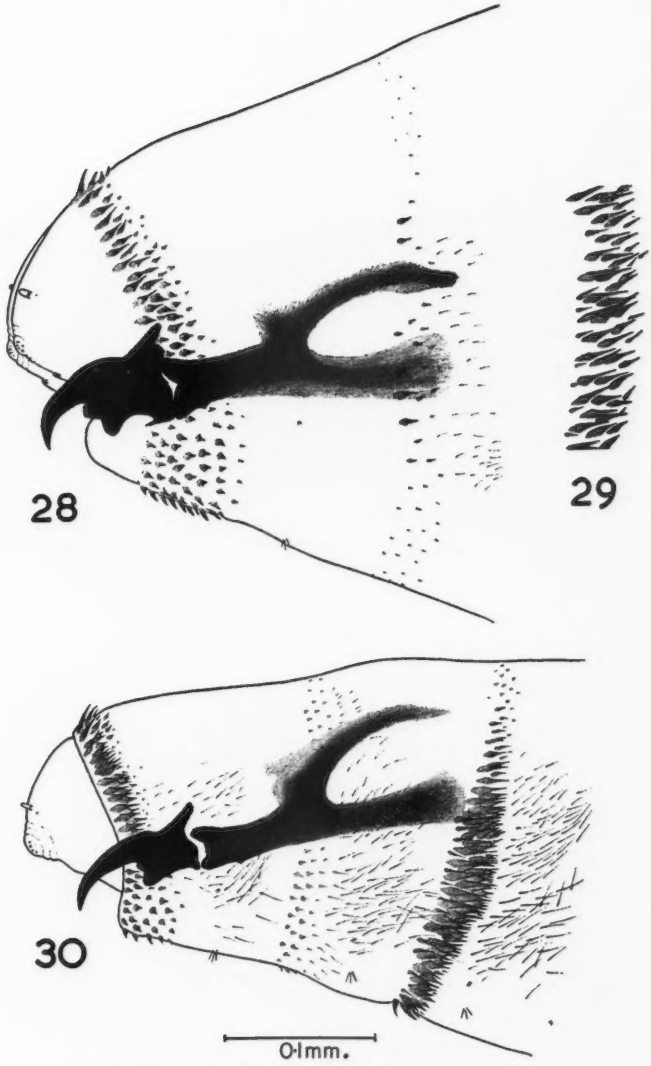


FIG. 18. *Acridiophaga aculeata, posterior segment.* FIG. 19. *Tephromyiella atlanis, a fusiform area on venter.* FIG. 20. *Tephromyiella neuquenensis, a fusiform area on venter.* FIG. 21. *Protodexia hunteri, posterior segments (dorsal).* FIG. 22. *Protodexia australis, posterior segments (dorsal).* FIG. 23. *Pricklelike spines (not to scale).*



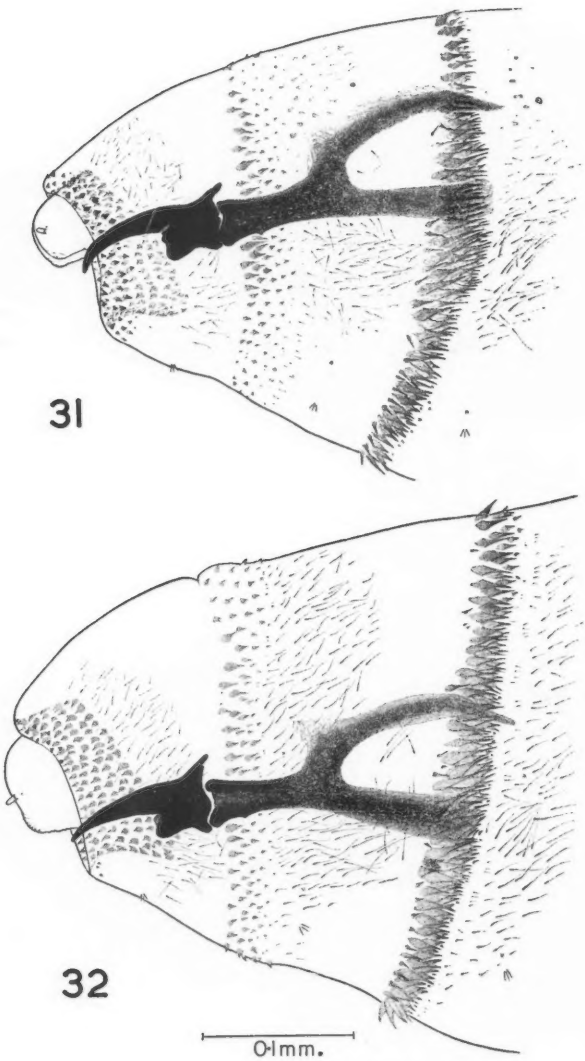
Second-instar Larva

FIG. 24. *Hemithrixion oestriforme.* FIG. 25. *Euacemyia tibialis.* FIG. 26. *Ceracia dentata.* FIG. 27. *Paradionaea atra (ventral).*

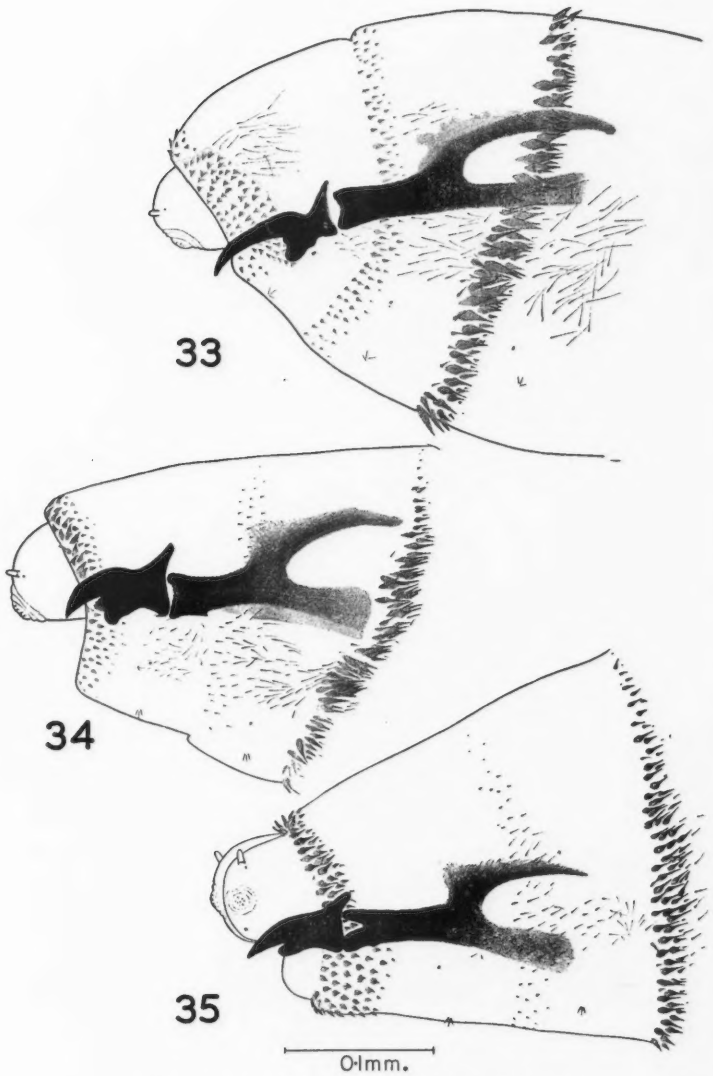


Buccopharyngeal Armature and Anterior Segments

FIG. 28. *Sarcophaga reversa.* FIG. 29. *Same, section of spines on Segment 3.* FIG. 30. *Sarcophaga* "H".

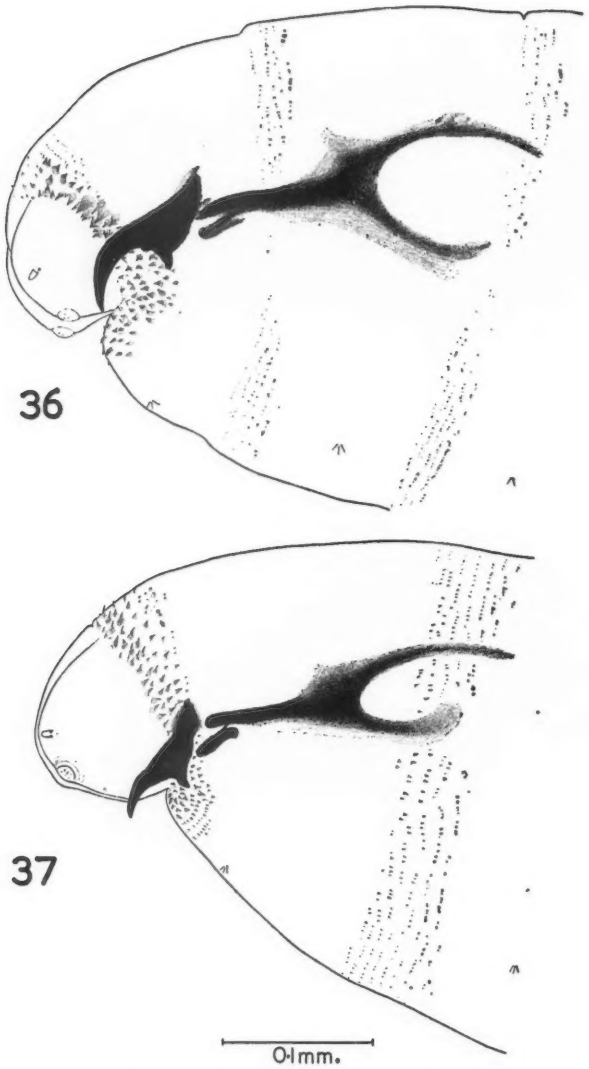


Buccopharyngeal Armature and Anterior Segments
FIG. 31. *Sarcophaga* "C". FIG. 32. *Sarcophaga* "E".



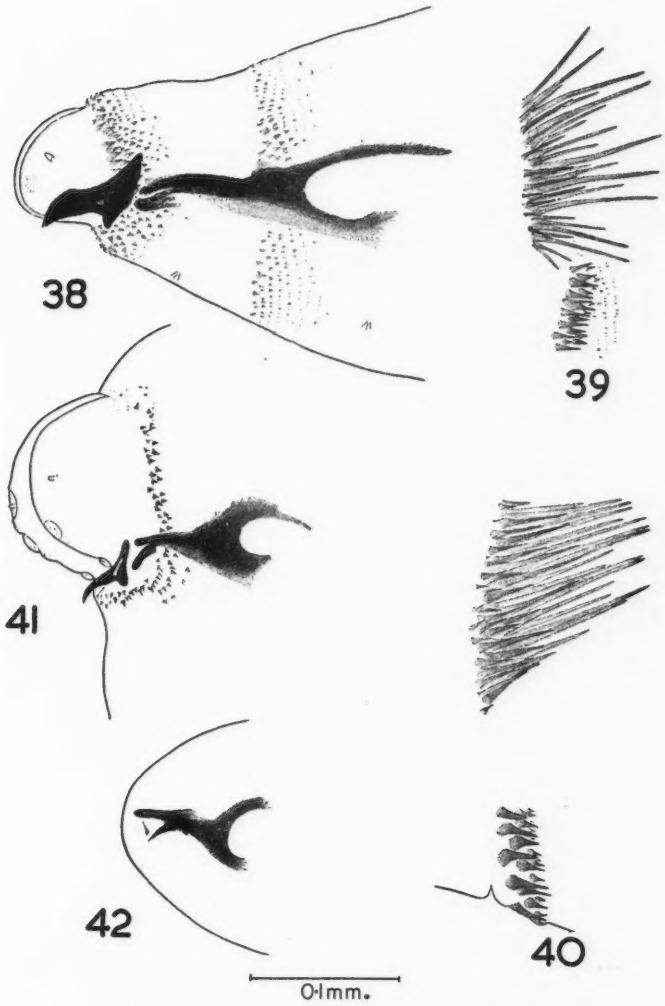
Buccopharyngeal Armature and Anterior Segments

FIG. 33. *Sarcophaga* "D". FIG. 34. *Acridiophaga caridei*. FIG. 35. *Acridiophaga aculeata*.



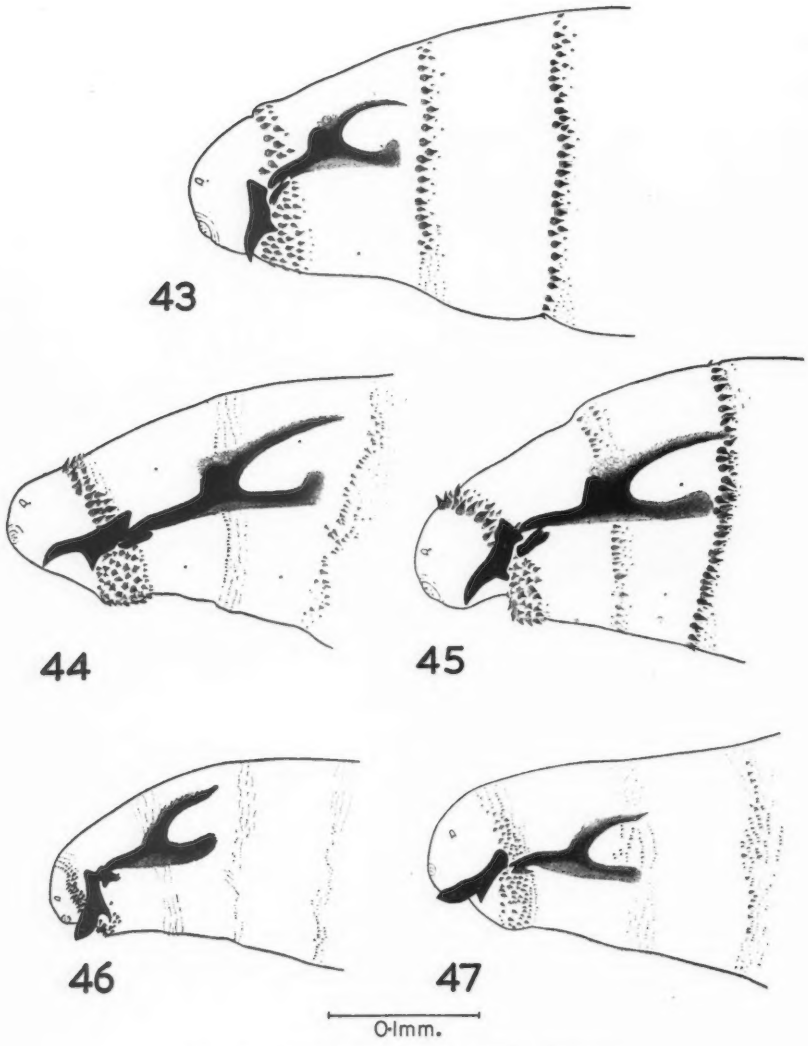
Buccopharyngeal Armature and Anterior Segments

FIG. 36. *Blaesoxiphotheca coloradensis.* FIG. 37. *Blaesoxiphotheca* "A".



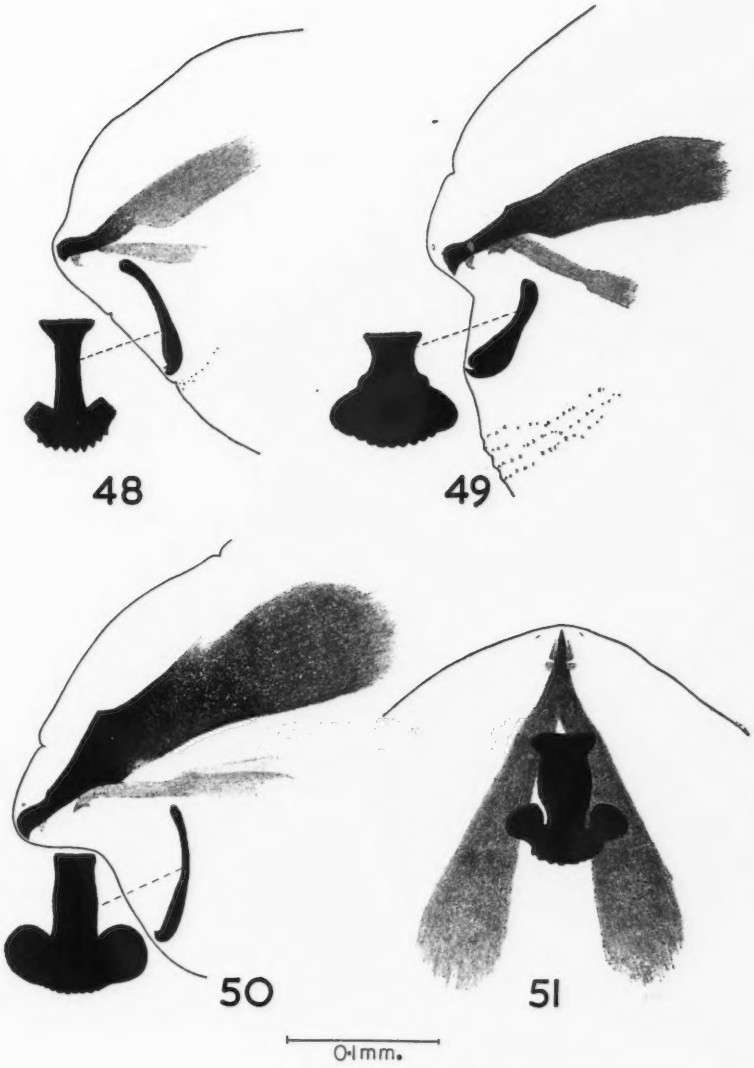
Buccopharyngeal Armature and Anterior Segments

FIG. 38. *Blaesoxiphotheca caudata.* FIG. 39. *Same, showing long lateral spines.* FIG. 40. *Long lateral spines of B. coloradensis.* FIG. 41. *Opsophyto opifera.* FIG. 42. *Acridomyia canadensis.*



Buccopharyngeal Armature and Anterior Segments

FIG. 43. *Tephromyiella* "A". FIG. 44. *Tephromyiella neuquenensis*. FIG. 45. *Tephromyiella atlanis*. FIG. 46. *Protodexia hunteri*. FIG. 47. *Protodexia australis*.



Buccopharyngeal Armature

FIG. 48. *Hemithrixion oestriforme.* FIG. 49. *Euacemyia tibialis.* FIG. 50. *Ceracia dentata.* FIG. 51. *Paradionaea atra (ventral).*

Commonwealth Agricultural Bureaux

This organization was set up by the Government of Canada in collaboration with the other Governments and responsible authorities of the British Commonwealth to provide up-to-date information in the form of journals, technical communications, and bibliographies on all aspects of science and practice as applied to agriculture, horticulture, and forestry.

JOURNALS. The following list comprises journals and other periodical publications. Subscription rates are quoted after each; in certain cases (journal marked with an asterisk) a 20 per cent deduction is made for subscribers in the British Commonwealth who send their subscriptions direct.

Bulletin of Entomological Research	(40s.)	Dairy Science Abstracts*	(35s.)
Review of Applied Entomology (Series A)	(40s.)	Forestry Abstracts*	(45s.)
Review of Applied Entomology (Series B)	(20s.)	Forest Products and Utilization	(15s.)
Review of Applied Mycology*	(40s.)	Horticultural Abstracts*	(35s.)
Helminthological Abstracts	(35s.)	Field Crop Abstracts*	(35s.)
Animal Breeding Abstracts*	(35s.)	Herbage Abstracts*	(35s.)
Veterinary Bulletin	(40s.)	Plant Breeding Abstracts*	(35s.)
Index Veterinarius	(100s.)	Soils and Fertilizers*	(35s.)
Nutrition Abstracts and Reviews	(63s.)		

OCCASIONAL PUBLICATIONS

	PRICE
Phenothiazine 1942-46: a Review and Bibliography. 1947.	4s.
Pregnancy Diagnosis Tests: a Review. 1948.	15s.
List of Recorded Cotton Insects of the World. 1948.	5s.
Report of the Fifth Commonwealth Entomological Conference, 22nd-30th July, 1948.	7s. 6d.
Diet in Relation to Reproduction and the Viability of the Young. Part I. Rats and other Laboratory Animals. 1948.	6s.
Gestation Periods. 2nd edn. 1947.	3s.
The Semen of Animals and its use for Artificial Insemination. 1945.	7s. 6d.

All correspondence regarding above journals and other publications may be addressed in the first instance to:

COMMONWEALTH AGRICULTURAL BUREAUX,
CENTRAL SALES BRANCH,
PENGLAIS,
ABERYSTWYTH, GREAT BRITAIN.

CANADIAN JOURNAL OF RESEARCH

Notes on the Preparation of Copy

GENERAL:—Manuscripts should be typewritten, double spaced, and the **original and one extra copy** submitted. Style, arrangement, spelling, and abbreviations should conform to the usage of this Journal. Names of all simple compounds, rather than their formulae, should be used in the text. Greek letters or unusual signs should be written plainly or explained by marginal notes. Superscripts and subscripts must be legible and carefully placed. Manuscripts should be carefully checked before being submitted, to reduce the need for changes after the type has been set. If authors require changes to be made after the type is set, they will be charged for changes that are considered to be excessive. **All pages, whether text, figures, or tables, should be numbered.**

ABSTRACT:—**An abstract of not more than about 200 words, indicating the scope of the work and the principal findings, is required.**

ILLUSTRATIONS:

(i) *Line Drawings:*—All lines should be of sufficient thickness to reproduce well. Drawings should be carefully made with India ink on white drawing paper, blue tracing linen, or co-ordinate paper **ruled in blue only**; any co-ordinate lines that are to appear in the reproduction should be ruled in black ink. Paper ruled in **green, yellow, or red should not be used** unless it is desired to have all the co-ordinate lines show. Lettering and numerals should be neatly done in India ink preferably with a stencil **(do not use typewriting)** and be of such size that they will be legible and not less than one millimetre in height when reproduced in a cut three inches wide. All experimental points should be carefully drawn with instruments. Illustrations need not be more than two or three times the size of the desired reproduction, but the ratio of height to width should conform with that of the type page. **The original drawings and one set of small but clear photographic copies are to be submitted.**

(ii) *Photographs:*—Prints should be made on glossy paper, with strong contrasts; they should be trimmed to remove all extraneous material so that essential features only are shown. Photographs should be submitted **in duplicate**; if they are to be reproduced in groups, one set should be so arranged and mounted on cardboard with rubber cement; the duplicate set should be unmounted.

(iii) *General:*—**The author's name, title of paper, and figure number should be written in the lower left hand corner (outside the illustration proper) of the sheets on which the illustrations appear.** Captions should not be written on the illustrations, but typed on a separate page of the manuscript. All figures (including each figure of the plates) should be numbered consecutively from 1 up (arabic numerals). **Each figure should be referred to in the text.** If authors desire to alter a cut, they will be charged for the new cut.

TABLES:—Titles should be given for all tables, which should be numbered in Roman numerals. Column heads should be brief and textual matter in tables confined to a minimum. **Each table should be referred to in the text.**

REFERENCES:—**These should be listed alphabetically by authors' names, numbered in that order, and placed at the end of the paper.** The form of literature citation should be that used in the respective sections of this Journal. **Titles of papers should not be given in references listed in Sections A, B, E, and F, but must be given in references listed in Sections C and D.** The first page only of the references cited in papers appearing in Sections A, B, and E should be given. **All citations should be checked with the original articles.** Each citation should be referred to in the text by means of the key number; in Sections C and D the author's name and the date of publication may be included with the key number if desired.

The *Canadian Journal of Research* conforms in general with the practice outlined in the *Canadian Government Editorial Style Manual*, published by the Department of Public Printing and Stationery, Ottawa.

Reprints

Fifty reprints of each paper without covers are supplied free. Additional reprints, if required, will be supplied according to a prescribed schedule of charges. On request, covers can be furnished at cost.